THE GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES *

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Tribe ROSEAE

17. Rosa Linnaeus, Sp. Pl. 1: 491. 1753; Gen. Pl. ed. 5. 217. 1754.

Mostly deciduous shrubs with upright, arching, trailing, or climbing stems; armature of stem, petiole, rachis, inflorescence branches, and floral cup of variously sized and shaped prickles and/or bristles (acicles), rarely absent; indumentum of simple hairs and/or sessile to stalked glands, variable in density and distribution. Leaves petiolate, imparipinnate or trifoliolate [very rarely simple]; leaflets toothed, the lateral ones nearly sessile, the terminal one long-petiolulate; stipules paired, conspicuous [rarely absent], entire to pinnatifid, sometimes fringed with glands, commonly adnate to the base of the petiole and forming wings, usually persistent. Inflorescences of few- to many-flowered, bracteate, determinate "corymbs" or "panicles" terminating primary or lateral stems, or the flowers solitary; flowers produced mostly on short shoots from the growth of last year. Flowers perfect, 5 (rarely 4) -merous, large, showy, often fragrant. Calyx without an epicalyx, the lobes quincuncial in aestivation, persistent or not, all entire or the outer two and half of the middle lobe fringed, toothed, or pinnatifid or with lateral appendages,[9] the apices acute to long attenuate or dilated; floral cups urceolate to globose, campanulate, or nearly tubular, the opening usually constricted; disc commonly prominent, forming a ring around the opening of the floral cup. Petals 5 (to numerous in double-flowered forms), white, yellow, or various shades of pink [orange or nearly red], narrowly to broadly obovate, the apices usually emarginate, tapering at the base, inserted at the outer edge of the disc. Androecium of many stamens in several whorls, the outer ones longer than the inner; filaments slender, persistent; anthers small, yellow. Gynoecium of numerous sessile or stipitate carpels included within and inserted at the base of, or on the inner walls of, the floral cup; styles terminal, shortly or long exserted beyond the mouth of the floral cup, free

* Continued from volume 55, p. 401.

[9] This type of aestivation has been noted in verse:

On a summer's day, in sultry weather,
Five brethren were born together.
Two had beards and two had none,
And the other had but half a one.

For other versions of this poem in English, Latin, and German, see Stearn and Bell.

below and free or connate into a column above; stigmas terminal, discoid, often tightly grouped together into a button-shaped structure blocking the opening of the floral cup; each carpel with one anatropous pendulous ovule. Fruit accessory (a hip), of numerous achenes enclosed by the enlarged, fleshy, usually red floral cup; achene wall hard; seed coat thin; embryo filling the seed and achene, the radicle superior. Base chromosome number 7. LECTOTYPE SPECIES: *R. centifolia* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. 2: 282. 1913.[10] (The ancient Latin name.) — ROSE.

About 120 or more species (several thousand described) in four subgenera of the Northern Hemisphere, extending from the arctic and boreal regions southward in North America to central Florida, Texas, Mexico, and Baja California, and in Eurasia to the Philippine Islands, Burma, southern India, and Persia, as well as in Ethiopia, and Mediterranean Africa. The largest concentration of species is in the region between western Asia and China. Members of the genus usually inhabit borderland or open habitats, such as fence rows, roadsides, scrublands, pastures, and the edges of woods. Because of the variability within species and the weak barriers to interspecific hybridization, the taxonomy of the genus is confusing, and many morphological variants have been described as distinct species. Several subgeneric classification schemes have been proposed (see Herring, 1925); the one outlined by Crépin (1889) and adopted by Rehder is accepted today as best reflecting natural relationships within the genus.

Most species of the genus are in cultivation, and in many ways the genus is remarkably well known. The chromosome numbers for most species have been reported, and some hybridization, breeding, and genetic studies have been made. However, nearly all the taxonomic investigations were done much earlier, were based primarily on cultivated plants, and had a strong horticultural emphasis. A modern review needs to be made with particular attention given to the species as they occur in nature; the Chinese species are particularly in need of study.

Only about 12 species, representing three sections of subg. ROSA are native to eastern North America, although more than a hundred have been described from this region; four species are indigenous to our area. Species belonging to all four subgenera and to all ten sections of subg. ROSA are cultivated in the southeastern United States, and some of these persist, become naturalized, or hybridize with native plants.

[10] Two other species, belonging to two other sections, have been proposed as the type species: *R. cinnamomea* L. (Rydberg, N. Am. Fl. 22: 483. 1918) and *R. canina* L. (Rehder, Bibliogr. Cult. Trees Shrubs, 296. 1949). Objections can be raised against the selection of any of these species: *R. centifolia* is not a wild species but a complex hybrid involving four species, *R. rubra*, *R. phoenicia*, *R. moschata*, and *R. canina* (see Hurst, 1941); *R. cinnamomea* clearly does not agree with the protologue with regard to the calyx lobes; and *R. canina* "is unsuitable as the name has been used in different senses by different authors" (Hitchcock & Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 1929). However, all of these are clearly members of this genus.

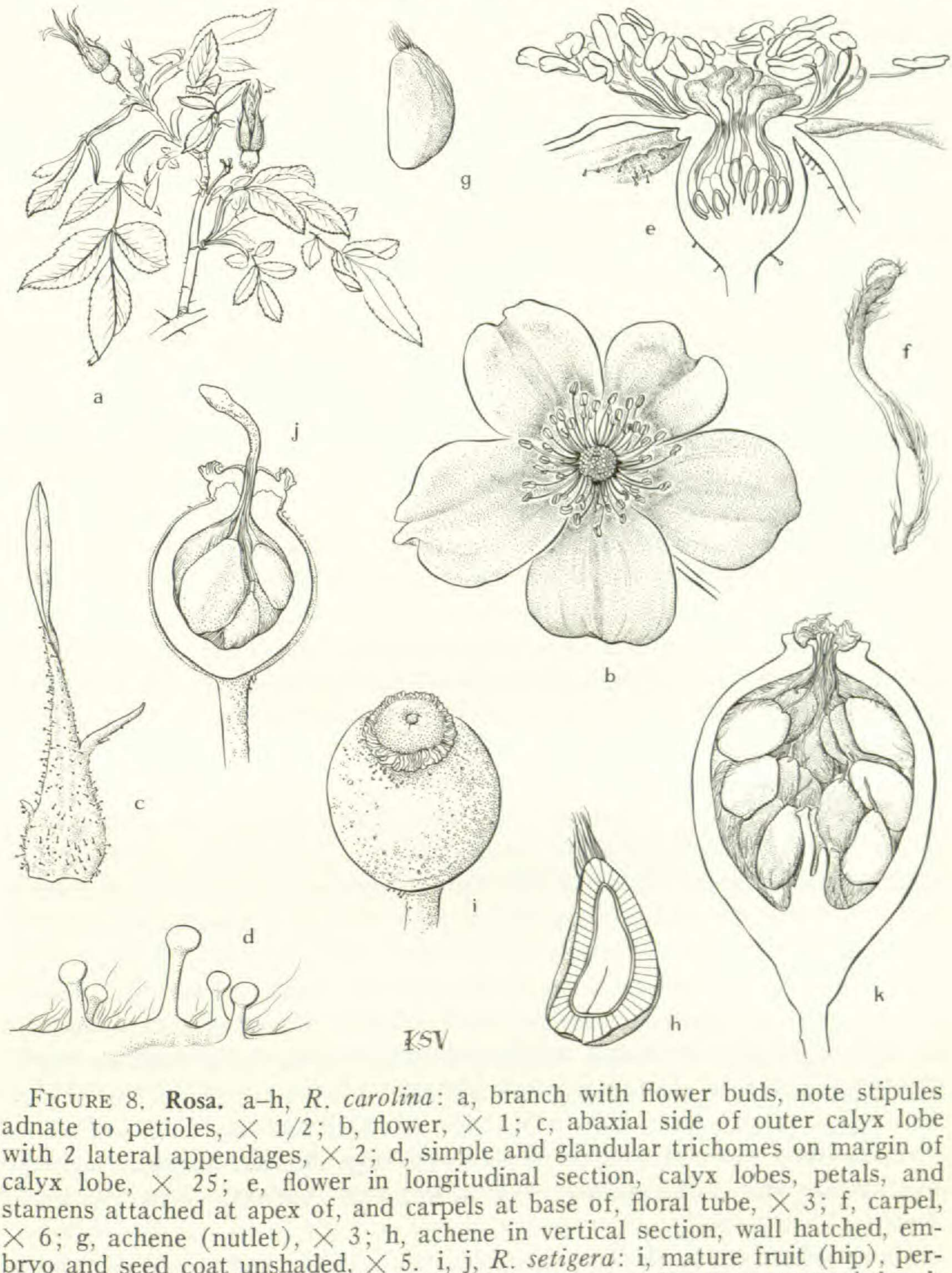

FIGURE 8. **Rosa.** a–h, *R. carolina*: a, branch with flower buds, note stipules adnate to petioles, × 1/2; b, flower, × 1; c, abaxial side of outer calyx lobe with 2 lateral appendages, × 2; d, simple and glandular trichomes on margin of calyx lobe, × 25; e, flower in longitudinal section, calyx lobes, petals, and stamens attached at apex of, and carpels at base of, floral tube, × 3; f, carpel, × 6; g, achene (nutlet), × 3; h, achene in vertical section, wall hatched, embryo and seed coat unshaded, × 5. i, j, *R. setigera*: i, mature fruit (hip), persistent filament bases surrounding disc with stylar scar in center, × 3; j, longitudinal section of fruit, styles connate into column above disc, × 3. k, *R. Eglanteria*: longitudinal section of mature fruit, carpels attached to wall at various levels, × 2.

The great majority of species of *Rosa* belong to subg. ROSA (floral cups glabrous or with glands or bristles, not with prickles), which is subdivided into ten sections. Three of our native roses, *R. carolina, R. palustris,* and *R. foliolosa,* belong to sect. CAROLINAE Crépin (carpels inserted at the base of the floral cup; calyx lobes deciduous from the hip, elongate, apically dilated and flattened, the outer with a few linear appendages or entire; floral cups glandular), which is restricted to eastern North America. Because each of the distinguishing characters of this section is found in some species of sect. CINNAMOMEAE DC., sect. CAROLINAE is sometimes merged with that section (see discussion in Lewis, 1957b).

Rosa carolina L., $2n = 28$, a variable and taxonomically complex species, occurs from peninsular Florida, Alabama, Mississippi, Louisiana, and Texas, northward to New England, Nova Scotia, and Ontario to Michigan, Wisconsin, and Nebraska. This species, distinguished from related ones by the fine and mostly straight infrastipular prickles that are round in cross section and not particularly broad based, the usual abundance of internodal prickles and bristles, the narrow stipular auricles (less than 2.5 mm. wide), the mostly solitary flowers, and the ovate or elliptic leaflets that are usually glabrous above and below, is particularly variable in the height of the plants, flower size, abundance of prickles, leaflet size, and indumentum density. Many of these characters can be altered by the environment, and *R. carolina* is one of the most heterogeneous roses of eastern North America. Segregate species ascribed to our area include *R. Lyonii* Pursh; *R. serrulata* auct., not Raf.; *R. subserrulata* Rydb.; *R. Treleasei* Rydb.; and *R. texarkana* Rydb. Toward the northern part of its range, *R. carolina* is sympatric with and hybridizes with *R. virginiana*, as it does toward the western part of its range with *R. arkansana* Porter.

Along the Atlantic seaboard from Newfoundland and New England to New Jersey, Delaware, and eastern Pennsylvania, there are a number of rather homogeneous populations of roses with stout, usually curved, broad based infrastipular prickles on the floral branches (but few or no internodal prickles or bristles), inflorescences of three or more flowers, apically dilated stipular auricles more than 2.5 mm. wide, obovate, shiny leaflets, and a sporophytic chromosome number of 28; these plants are properly called *Rosa virginiana* L. Similar, more variable plants with at least some of these features are found southward and westward to Virginia, North Carolina, Alabama, Tennessee, and Missouri; these are either included in *R. virginiana* (Fernald, Gray's Manual, ed. 8; Steyermark, Fl. Missouri) or considered to be the result of hybridization and introgression between *R. carolina* and *R. virginiana* or *R. arkansana* (Gleason, New Britton & Brown; Lewis, 1958).

Rosa palustris Marshall, swamp rose, $2n = 14$, a tall shrub with finely toothed leaflets, convolute stipules, and large, stout infrastipular prickles (but lacking internodal prickles and bristles), ranges from Florida to Arkansas, north to Nova Scotia, Ontario, Michigan, Wisconsin, and Minnesota; it is especially common along the Atlantic seaboard. As the specific and common names indicate, this species is largely restricted to wet habitats, such as swamps, marshes, wet woods, and the borders of streams, bayous, sink holes, and drainage ditches. Plants with fewer (usually 5) and smaller leaflets and depressed-globose, instead of globose or ellipsoidal, floral cups have been separated as *R. floridana* Rydb.

The other species of sect. CAROLINAE in our area is *R. foliolosa* Nutt. ex Torrey & Gray, $2n = 14$, a distinctive low shrub of dry, open areas, mostly with nine, narrow, elliptic leaflets per leaf and stems that are unarmed or have a few small, straight prickles. This species has one of the narrowest distributions of any native North American rose: extreme western Arkansas, the eastern two-thirds of Oklahoma, and central and north-central Texas. *Rosa nitida* Willd., $2n = 14$, the only other species of this section, occurs in New England, Quebec, and the Maritime Provinces of Canada.

The largest section of the genus is sect. CINNAMOMEAE DC. (sect. *Cassiorhodon* Dumort.) (erect, deciduous shrubs with bristles and usually slender, straight prickles in infrastipular pairs or scattered; flowers numerous, in bracteate corymbs; calyx lobes persistent, all entire; carpels lining the sides of the floral cup), which includes more than fifty species of both hemispheres. Although this section does not occur in our area, four species are indigenous to North America, and *Rosa rugosa* Thunb., $2n = 14$, a native of eastern Asia, has become thoroughly naturalized within the past 70 years along beaches from the Bay of Fundy to Long Island Sound and New Jersey and also around the lower Great Lakes.

Our only other indigenous rose is *Rosa setigera* Michx., prairie rose, $2n = 14$, the only New World species of sect. SYNSTYLAE DC. (styles exserted, united into a column). This plant, a large shrub with long (to 5 m. or more), climbing, leaning, or trailing stems, trifoliolate leaves (the leaflets large, coarsely toothed), uniform-sized infra- and internodal prickles (but no bristles), and glandular stipules, petioles, pedicels, calyx lobes, and floral cups, is indigenous to the region from northeastern Texas, Oklahoma, Kansas, and Nebraska, east to the eastern foothills of the Appalachians. It has become naturalized along the Atlantic seaboard from New England to South Carolina. Two varieties, var. *setigera*, with the leaflets glabrous below or with trichomes only on the veins, and var. *tomentosa* Torrey & Gray, with the leaflets pubescent below, can be distinguished. Unarmed plants of both varieties occur, as do white-flowered individuals of var. *tomentosa*.

Two eastern Asiatic species of sect. SYNSTYLAE are naturalized in eastern North America. *Rosa multiflora* Thunb., $2n = 14$, Japanese or multiflora rose, an arching or trailing shrub with numerous small flowers in pyramidal inflorescences, fimbriate-pectinate stipules, glabrous styles, and only infrastipular prickles, is commonly planted along fence rows and roadsides, particularly as a "living fence." It is reproducing by seed from New England and New York, south and west to the Carolinas, Mississippi, Tennessee, Missouri, Oklahoma, and Texas. The memorial rose, *R. Wichuraiana* Crépin, $2n = 14$, a low, semi-evergreen plant with long, prostrate or trailing branches, pubescent styles, jagged-dentate stipules, and scattered prickles, is often grown as a ground cover along highways and railroads, and it has spread locally in at least Virginia, the Carolinas, and Ohio.

Rosa laevigata Michx., $2n = 14$, Cherokee rose, the only species of sect. LAEVIGATAE Crépin, was for some time thought to be indigenous to the southern United States (Michaux described it from plants collected in Georgia), but it is actually a Chinese plant that was introduced and became naturalized at an early date. This distinctive species is a high-climbing shrub with evergreen, glossy, ternately compound leaves; large, white, solitary flowers; bristly floral cups, pedicels, and hips; and uniform curved internodal and infranodal prickles.

Rosa bracteata Wendl., $2n = 14$, of sect. BRACTEATAE Crépin (stems, inflorescence branches, and floral cups tomentose; flowers few or solitary, short-stalked, subtended by large, foliaceous bracts; stipules pectinate; infrastipular prickles stout, curved; internodal regions mostly with bristles and stipitate glands) is a native of China and Taiwan that is commonly planted in the southern United States as a "living fence"; it readily escapes and is naturalized from Florida to Texas, northward to Virginia and Tennessee. This is a handsome shrub with long, stout branches that clamber, ramble, or recline (sometimes forming mounds 5 m. or more tall), large white flowers, and evergreen leaves with 5 to 9 small, leathery, glossy leaflets. The only other species of this section is *R. clinophylla* Thory, of India.

Section CANINAE DC., dog roses, includes deciduous shrubs with numerous, uniform-sized prickles (bristles mostly absent), usually pinnate outer calyx lobes, and long stipitate carpels. This group is nearly confined to Europe and is taxonomically quite difficult. Three species have escaped from cultivation locally in the eastern United States: *Rosa Eglanteria* L.,[11] $2n = 35$, sweet briar (leaflets pubescent and densely glandular below, styles villous or lanate, calyx lobes persistent); *R. micrantha* Smith (similar to the preceding but the styles glabrous); and *R. canina* L., $2n = 35$, dog rose (leaflets glabrous and eglandular below, calyx lobes caducous).

All species of sect. CANINAE are polyploid (mostly pentaploids), as far as is known, and they have a type of reproduction that is unlike that of any other flowering plant. During meiosis, 7 bivalents and 14, 21, or 28 univalents are formed. The univalents are not incorporated into pollen grains, which have 7 chromosomes. The megaspores, however, contain all of the univalents plus a set of 7 chromosomes from the bivalents. At fertilization the original, parental chromosome number is restored. Thus in pentaploid species, the pollen contains 7 chromosomes, while the egg cells have 28 chromosomes. Inheritance is strongly maternal, and reciprocal hybrids between species result in plants differing in chromosome inheritance. A hybrid of *R. canina* and *R. Eglanteria* can be 4/5 *canina* and 1/5 *Eglanteria* or *vice versa*. This mechanism is genetically controlled and can be broken down when crosses are made with species belonging to other sections.

[11] In some European floras *R. Eglanteria* L., Sp. Pl. **1**: 491. 1753, is considered an ambiguous name and is replaced by *R. rubiginosa* L., Mantissa Alt. 564. 1771.

Section ROSA (erect, low, deciduous, rhizomatous shrubs with bristles and hooked prickles; flowers often solitary, without subtending bracts; calyx lobes deciduous, the outer pinnate; carpels sessile) includes one wild species, *Rosa gallica* L., $2n = 28$, French rose, Provins rose, red rose of Lancaster, a native of southern and central Europe that occasionally persists or escapes from cultivation in the eastern United States. This species has given rise by mutation and hybridization to several groups of "old garden roses": damask roses (*R. damascena* Miller), cabbage roses (*R. centifolia* L.), moss roses (*R. centifolia* var. *muscosa* (Miller) Ser.), and alba roses (*R. alba* L.).

The remaining sections of subg. ROSA are PIMPINELLIFOLIAE DC. (about 10 Old World species), CHINENSES DC. (two species of China), and BANKSIAE Crépin (*R. Banksiae* Aiton, China). The other subgenera are HULTHEMIA (Dumort.) Focke (*R. persica* Michx. ex J. F. Gmelin, southwestern and central Asia), PLATYRHODON (Hurst) Rehder (*R. Roxburghii* Tratt., China and Japan), and HESPERHODOS Rehder (*R. stellata* Wooton, New Mexico and Texas; *R. minutifolia* Engelm., northern Baja California).

The genus has been studied cytologically in some detail. The base chromosome number is 7 (aneuploidy is known only in cultivars) and the chromosomes are small and morphologically similar to one another, differing mostly in number and behavior at meiosis. The species of subgenera HULTHEMIA, PLATYRHODON, and HESPERHODOS and sects. SYNSTYLAE, CHINENSES, BANKSIAE, LAEVIGATAE, and BRACTEATAE of subg. ROSA are all diploid. Sections PIMPINELLIFOLIAE and CAROLINAE have diploid and tetraploid species; CINNAMOMEAE, diploid, tetraploid, hexaploid, and octoploid species; GALLICANAE, one tetraploid species; and CANINAE, heterogamous polyploid species. Täckholm (see map in Hurst, 1928) showed that in Europe there is a regular series of ploidy levels from south (diploid) to north (octoploid). A somewhat similar phenomenon seems to occur in North America, with the octoploid *Rosa acicularis* subsp. *acicularis* in Alaska and the hexaploid subsp. *Sayi* in northern North America (extending southward in the Rocky Mountains). Tetraploid and diploid species are widely distributed, but the diploids do occur farther south than the tetraploids (see map in Lewis, 1970).

Roses have long been one of the favorite flowers of peoples of many lands and cultures, and they often figure in song, poetry, literature, and painting. Historical events, such as the War of Roses, are sometimes associated with the genus. The common garden roses are of complex hybrid origin involving *Rosa chinensis* Jacq., *R. odorata* (Andrews) Sweet, *R. gallica*, *R. moschata* Herrm., *R. foetida* Herrm., *R. multiflora*, and *R. Wichuraiana*. Rose hips are flavorful, contain a large concentration of vitamin C, and are sometimes eaten fresh or made into jelly or tea. *Rosa damascena* is grown commercially in Bulgaria, France, and the Middle East for the production of Attar of roses and rose water.

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Subfam. MALOIDEAE C. Weber

(Subfam. Pomoideae, nom. invalid.)

A very natural group of perhaps 19 genera of the Northern Hemisphere. Only four genera, *Chamaemeles* Lindley (monotypic, Madeira), *Hesperomeles* Lindley (15 spp., Central and South America, often included in *Osteomeles* Lindley), *Heteromeles* Roemer (monotypic, California and Baja California; sometimes included in *Photinia* Lindley), and *Peraphyllum* Nutt. ex Torrey & Gray (monotypic, western United States), do not have species in Asia. Three genera, *Amelanchier* Medicus, *Pyrus* L. (including *Malus, Sorbus,* and *Aronia*), and *Crataegus* L., have species indigenous to eastern North America, and *Pyracantha* Roemer is naturalized in that region.

Two tribes are sometimes recognized, Crataegeae Koehne with the inner walls of the carpels becoming hard and each carpel developing into a separate nutlet (the fruit called by Kalkman a polypyrenous drupe) and Sorbeae Koehne with the inner walls of the carpels becoming chartaceous or cartilaginous, rarely bony, and the carpels laterally connate (the fruit with one multilocular "core"). Tribe Crataegeae includes *Chamaemeles, Cotoneaster* Ehrh., *Crataegus* L., *Hesperomeles, Mespilus* L., *Osteomeles,* and *Pyracantha*; tribe Sorbeae includes *Amelanchier, Chaenomeles* Lindley, *Cydonia* Miller, *Dichotomanthes* Kurz, *Docynia* Decaisne, *Eriobotrya* Lindley, *Heteromeles, Peraphyllum, Photinia, Pyrus, Rhaphiolepis* Lindley corr. Poiret, and *Stranvaesia* Lindley. The characters of the consistency (induration) of the endocarp and the degree of lateral connation of the carpels seem to be more variable than originally thought, and the division of the subfamily into two tribes as outlined above may not best reflect generic relationships.

Generic limits are notoriously difficult to define in subfam. Maloideae. On morphological grounds alone, it would not be difficult to distinguish

30 genera. The flowers and fruits of all species of the subfamily are quite similar, but there are numerous variations (often difficult to see on herbarium specimens). Some floral differences are the type and position of inflorescences, the number of flowers, the arrangement of the calyx lobes at anthesis, the color of the petals, the number of stamens and staminal whorls, the number of carpels, the degree of adnation of the carpels to the floral cup, the degree of connation of the styles, the shape of the stigmas, and the number of ovules. Fruits differ in color, shape, and size, the presence or absence of grit cells, the consistency and degree of lateral connation of the inner carpel walls, and the persistence of the calyx lobes. *Pyrus* subg. SORBUS is particularly critical, since within it are found many of the characters used to delineate the other genera. Barriers to hybridization between both species and genera are usually weak. Hybrids between *Pyrus* subg. SORBUS and *Amelanchier, Cotoneaster, Crataegus, Mespilus* (see Kovanda), and *Pyrus* subg. ARONIA, subg. MALUS, and subg. PYRUS are known. Also reported are hybrids between *Crataegus* and *Mespilus*; *Crataegus* and *Pyrus* subg. PYRUS; *Pyracantha* and *Osteomeles*; *Pyracantha* and *Cotoneaster*; *Cydonia* and *Pyrus* subg. PYRUS; *Cydonia* and *Pyrus* subg. MALUS (see Rehder); and *Pyrus* subg. PYRUS and *P.* subg. MALUS. Sax (1931, subfam. ref.) went so far as to say that on genetic and cytological grounds "all of the present genera of the Pomoideae might be classed as genetic species under one genus. In at least one case two genera [*Sorbus* and *Aronia*] should be combined in one species." It does not seem likely that a universally acceptable system of generic delimitation can be devised in the forseeable future.

Most Maloideae have partly to completely inferior ovaries that develop into characteristic fruits, pomes, in which the carpels are practically surrounded by the enlarged, usually fleshy floral cup. The nature of the inferior ovary, floral cup, and fruit is debatable. According to the "axial" or "receptacular" theory, the carpels are sunken in the pith of the invaginated stem, so the flesh of the pome is largely receptacular in origin (see Black and Tukey & Young under *Pyrus*). The "appendicular" theory holds that the floral cup consists of the adnate bases of the sepals, petals, and stamens, and the fleshy part of the fruit is thus appendicular (see MacDaniels and Blaser & Einset, *Pyrus* ref.). In a recent Hungarian investigation of the pear (Gracza, *Pyrus* ref.), both axial and appendicular regions were identified in the mature fruit. Virtually all studies on the nature of the pome have been made on the cultivated apple or pear; other genera of Maloideae need to be investigated; perhaps then a definitive explanation of the maloidean floral cup can be given.

The base chromosome number in the Maloideae is 17, a number unknown in other Rosaceae, except *Quillaja brasiliensis* (St. Hil.) Martius (Spiraeoideae-Quillajeae). Fifteen genera have been examined cytologically. The species of small genera are predominantly diploid, while tetraploid or triploid species (or hybrids) are common in large genera; higher polyploid levels and aneuploidy are quite rare. Several hypotheses have been proposed to explain the base number of 17: *Malus* is an aneuploid derived from a halved pentaploid ancestor that had a base number of seven ($x = 1/2\ (35 - 1)$; Nebel, *Pyrus* ref.); or the Maloideae are triple tetrasomics developed from a seven-chromosome type with four chromosomes represented twice and three chromosomes represented three times ($x = 8 + 8 + 1$; Sax, 1931, subfam. ref.); or the Maloideae are allotetraploids that arose from a cross between plants with base numbers of eight and nine and involving either two members of the Spiraeoideae or representatives of the Spiraeoideae and Rosoideae ($x = 8 + 9$; Sax, 1932, subfam. ref.); or the Maloideae are amphidiploids derived from hybridization of ancestral Spiraeoideae and Amygdaloideae ($x = 9 + 8$; Stebbins, subfam. ref.).

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18. **Pyracantha** M. J. Roemer, Fam. Nat. Reg. Veg. Syn. Monograph. 3: 104, 219. 1847.

Evergreen, compactly branched shrubs with slender but rigid stems, thorns (bearing leaves or leaf scars), and spine-tipped lateral branches; buds small, sessile, solitary or collaterally branched in spine formations, the scales dry. Leaves alternate, shortly petiolate; blades elliptic to obovate with crenate [serrate, or entire margins], the teeth often glandular tipped; leaf scars somewhat raised, narrowly crescent shaped or 3 lobed with 3 bundle traces; stipules minute, caducous. Inflorescences several-flowered compound cymes or corymbs terminating short lateral shoots. Flowers perfect. Calyx without an epicalyx, the 5 small lobes broadly triangular, sometimes glandular toothed, persistent, imbricate in aestivation; floral cup turbinate at anthesis. Petals 5, whitish, spreading, deciduous, equal, subcircular with uneven margins, the lower adaxial surfaces slightly pubescent, inserted at the edge of the floral cup, imbricate. Androecium of 20 stamens; filaments free except at the base, unequal in length, inserted in 2 series at the edge of the floral cup between the perianth and a fleshy nectar ring surrounding the mouth of the floral cup. Gynoecium of 5 antesepalous carpels, adaxially and laterally free but abaxially half-adnate to the floral cup (the ovaries half-inferior), the exposed upper surfaces densely pubescent; styles 5, terminal on the adaxial margins, deciduous; stigmas discoid; each carpel with 2 ascending, anatropous ovules on an adaxial and basal placenta, the micropyle inferior. Fruit a small, ± globose, orange to red pome [yellow or white in cultivars], open at the apex; carpels remaining distinct from each other, becoming stony and forming 2- or 1-seeded nutlets surrounded by the enlarged, fleshy floral cup crowned by the persistent calyx lobes; mature seed or seeds filling the nutlet cavity, the testa membranaceous, endosperm absent; embryo erect, the cotyledons plano-convex. Base chromosome number 17. LECTOTYPE SPECIES: *Mespilus Pyracantha* L. = *P. coccinea* Roemer; see A. Rehder, Bibliogr. Cult. Trees Shrubs, 239. 1949. (Name from Greek *pyr*, fire, and *acantha*, thorn, in reference to the red fruits and thorny branches.) — FIRETHORN.

A genus of about eight species, with *Pyracantha coccinea* in southern Europe and western Asia, *P. Koidzumii* Rehder in eastern Formosa, and five or more species in China (the greatest concentration of species in Yunnan) and Indochina. *Pyracantha crenulata* (Roxb.) Roemer var. *crenulata* occurs in the Himalayas as far east as Bhutan; other varieties of this species are disjunct in southwestern and northwestern China and North Vietnam. The genus is taxonomically straightforward (excluding cultivars) but needs a modern review to update nomenclature, clarify the status of a few taxa, and work out geographical distributions.

Pyracantha coccinea has escaped from cultivation and become locally naturalized in the eastern United States from Pennsylvania to Florida and Louisiana; it also persists near old house sites. This species is distinguished from others by the pubescent, but not tomentose, lower leaf surfaces, calyx lobes, floral cups, and pedicels and the elliptic to obovate leaf blades usually with crenulate-serrulate margins. Today *P. coccinea* occurs in the Old World from the Pyrénées to Italy, southeastern Europe, Turkey, Crimea, Caucasia, and Iran. Some authors believe that this species does not occur naturally west of Italy; others place the westernmost natural limit in Dalmatia. *Pyracantha Koidzumii* has recently been reported as escaped in Spartanburg Co., S. C. (Clark *et al.*, Castanea **38**: 300. 1973).

Pyracantha is closely related to *Cotoneaster* Medicus (in which it was included by Focke, Small, and Fernald), as well as to *Crataegus* L. It differs from the former in having thorns and usually serrate (rather than always entire) leaves and from the latter in its unlobed and evergreen (rather than lobed and deciduous) leaves, its caducous instead of partly persistent stipules, and its often two- rather than one-seeded nutlets. An intergeneric hybrid, × *Pyracomeles Vilmorinii* Rehder ex Guillaumin, arose spontaneously in a French nursery between *Pyracantha crenato-serrata* (Hance) Rehder and *Osteomeles subrotunda* K. Koch. A hybrid between *Pyracantha* and *Cotoneaster* has been obtained by W. E. Silva (cf. Egolf & Drechsler). The six species and many cultivars that have been examined cytologically have a chromosome number of $2n = 34$, the same as the majority of Maloideae.

Plants of *Pyracantha* are extensively grown as shrubs, hedges, or espaliers. They are particularly attractive in autumn when the colorful fruits mature. The species are reasonably distinct in nature, but in cultivation they hybridize readily, and true species are rarely found in gardens, since many nurseries raise the plants from seed of open-pollinated flowers.

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19. **Crataegus** Linnaeus, Sp. Pl. 1: 475. 1753; Gen. Pl. ed. 5. 213. 1754.

Deciduous or semi-evergreen shrubs or small trees, often much branched, with terete, slender but rigid and ± zigzag branches; usually armed with simple or branched axillary spines; bark scaly and/or deeply fissured and crosschecked, ashy gray to dark brown; buds small, subglobose, sessile, solitary or collaterally branched in spine formations, the outer scales brownish, the inner fleshy and green to red. Leaves alternate, petiolate; blades usually toothed (the teeth glandular tipped) and lobed or deeply divided, ovate to elliptic or obovate, leaves at ends of vegetative shoots usually larger, more deeply lobed and differently shaped than those of flowering branches; leaf scars slightly elevated, narrowly crescent shaped with 3 bundle-scars; stipules commonly glandular toothed, large and persistent on vegetative branches, or small and deciduous on flowering branches. Inflorescences few- to many-flowered, simple or compound, ± convex cymes terminating short lateral, leafy branches; bracts and bractlets linear, often brightly colored and glandiferous, caducous, leaving a prominent glandlike scar. Flowers perfect, 5-merous. Calyx without an epicalyx, the 5 lobes reflexed at anthesis, acute or acuminate, rarely foliaceous, often glandular-serrate and gland tipped, deciduous or persistent, imbricate in aestivation; floral tube cup shaped to urceolate at anthesis, adnate to the carpels. Petals white to light or dark pink, spreading, equal, subcircular with entire to erose margins, deciduous, inserted at the edge of the floral tube, imbricate. Androecium of 5–25 stamens, when 10, in one whorl of 5 pairs, when more than 10, the outer whorl consisting of 5 pairs; filaments free except at base, usually unequal in length, inserted on the rim of a small to prominent, fleshy nectar ring surrounding the mouth of the floral tube; anthers pale to intense yellow, pink, or purple. Gynoecium of 1–5 carpels, abaxially half to completely adnate to the floral cup (the ovaries half to completely inferior) and adaxially and laterally free to ± connate; styles as many as the carpels, distinct or weakly connate, terminal on the adaxial margins, persistent; stigmas discoid; each carpel with 2 erect, anatropous ovules on an adaxial and basal placenta, the micropyle inferior. Fruit red, orange, yellow, blue, or black, a small subglobose, ovoid, obovoid, or pyriform pome, slightly open at the apex with the persistent styles protruding; carpels remaining or becoming distinct from each other, forming stony, usually one-seeded nutlets surrounded by the enlarged, fleshy to mealy floral tube; mature seed filling nutlet cavity. Testa membranaceous; endosperm absent; embryo erect, the cotyledons planoconvex, the radicle short, inferior. LECTOTYPE SPECIES: *C. Oxyacantha* L.; see W. W. Eggleston in N. L. Britton, N. Am. Trees, 444. 1908.[12] (Name from Greek *krataigos*, a kind of flowering thorn, evidently applied by Theophrastus to a species of *Crataegus*, perhaps in turn derived from *kratos*, strength, alluding to the strong wood or the numerous thorns that protect the plants from browsing animals.) — HAWTHORN, THORN, HAW.

One of the taxonomically most difficult genera in the eastern United States with well over a thousand described "species." The actual number of biological entities worthy of taxonomic recognition is impossible to determine at present due to the large number of local variants that may be hybrids, apomicts, or both. The genus is most abundant, both as to individuals and diverse forms, in the region from Newfoundland westward through the St. Lawrence River basin to northwestern Minnesota and south to Florida and the mouth of the Colorado River in Texas. Relatively few species occur in the Rocky Mountains, the Pacific Coast region, through the highlands of Mexico to the Andes, and in Europe, the Middle East, central and southwestern Asia, Siberia, China, and Japan. The majority of *Crataegus* species are calciphilous and occur in somewhat disturbed habitats along the borders of streams, rocky ledges or woods, and in prairies, glades, copses, fence rows, and pastures. In our area nu-

[12] Medicus (Philosoph. Bot. 1: 150, 154, 155. 1789) referred this species to his genus *Oxyacantha*. It is debatable whether *Crataegus Oxyacantha* L. can then be designated as the lectotype species of *Crataegus*, although it appears that all subsequent authors have followed Eggleston's selection; the current Code of Botanical Nomenclature provides few guidelines for the lectotypification of generic names.

merous species are restricted to dry, sandy, upland woods with acidic soils; others inhabit swamps or rich, low, wet grounds.

The genus may be subdivided into about thirty series, but the exact number currently recognized is difficult to determine since there is no recent treatment of the genus on a worldwide basis (Rehder's *Bibliography* lists all series in cultivation). Additionally, there are varying concepts as to the criteria to be used in delimiting series and the species to be included, and the nomenclature is badly tangled. The author citations of the series need reviewing, since neither Beadle nor Sargent designated the rank of their subgeneric categories, although many of their names have been adopted. The morphological distinctiveness of the series varies considerably, some being clearly delimited (e.g., AESTIVALES (Sargent ex Palmer) Rehder; BREVISPINAE Beadle ex Rehder; MICROCARPAE (Loudon) Rehder; CORDATAE Beadle ex Rehder), while others have indefinite discontinuities between them (MOLLES (Sargent ex Palmer) Rehder; COCCINEAE (Loudon) Rehder; TENUIFOLIAE (Sargent ex Palmer) Rehder; DILATATAE (Sargent ex Palmer) Rehder; PUNCTATAE (Loudon) Rehder; VIRIDES (Beadle ex Palmer) Rehder; and PULCHERRIMAE (Beadle ex Palmer) Robertson).[13]

In his synopsis of North American hawthorns, Palmer listed about 300 species in 18 sections (and one group of unassignable species) as occurring in our area. In the second edition of Small's *Flora of the Southeastern United States* (1913), Beadle assigned 185 species to 33 infrageneric groups of undesignated rank, but Tidestrom distinguished only 33 species in 16 groups in Small's *Manual* (1933). Radford, Ahles, & Bell recognized 13 species in the Carolinas. These very diverse treatments are indicative of the problems encountered in *Crataegus*. While it is clearly beyond the scope of this paper to enumerate all taxonomic entities in our area, a few generalizations are possible.

Representatives of 21 series occur in the southeastern United States, to which several series are entirely or predominantly restricted (AESTIVALES; APIIFOLIAE (Loudon) Rehder; BRACTEATAE (Sargent ex Palmer) Rehder; BREVISPINAE; FLAVAE (Loudon) Rehder; MICROCARPAE; PULCHERRIMAE; TRIFOLIAE (Beadle ex Palmer) Rehder; and VIRIDES). Other series have a more northern or western primary distribution with only one or a few species occurring toward the periphery of our area (PRUINOSAE (Sargent ex Palmer) Rehder; TENUIFOLIAE). Not many series have species ranging throughout the eastern United States (CRUS-GALLINAE Rehder; MOLLES; PUNCTATAE), and no series or species has a transcontinental distribution.

The taxonomic and nomenclatural confusion in *Crataegus* today is a relatively recent phenomenon. Before the year 1896, fewer than 17 species and varieties were commonly recognized as occurring naturally or spon-

[13] *Crataegus* series **Pulcherrimae** (Beadle ex Palmer) Robertson, stat. nov. *Crataegus* sect. *Pulcherrimae* Beadle ex Palmer, Jour. Arnold Arb. **6**: 78, 79. 1925 (based on group "Pulcherrimae" of Beadle in Small, Fl. Southeast. U.S. 532. 1903).

taneously in the eastern United States. Then, during the first decade of the Twentieth Century, descriptions of new species appeared at a prodigious rate, largely as the result of the efforts of W. W. Ashe, of the U.S. Forest Service (who named at least 177 species), C. D. Beadle, of the Biltmore Herbarium (whose contribution amounted to 143), and C. S. Sargent, of the Arnold Arboretum (who added over 700). (See Sutton for an excellent account of Sargent's work with *Crataegus*). This plethora of new *Crataegus* species inevitably drew criticism (see Bessey and Camp). Because of the sheer numbers of taxa described, most subsequent authors and collectors have largely ignored the genus, considering the situation hopeless.

That numerous species described during what Palmer called "the period of expansion for the genus" are synonyms of previously described species is now clear, although the morphological variations that caused the deluge of descriptions are very real. The explanation usually advanced is that relatively few species are sexually reproducing diploids, the majority being triploids or other polyploids (sometimes derived by hybridization) that frequently set seed apogamously. This conclusion is based on the following evidence: there is a high incidence of pollen sterility among members of the genus; of the more than 130 representatives that are known cytologically, more than half are triploids and less than 25% are diploids; triploid and pollen-sterile plants often set seed that produce offspring very similar to the parent plants; and flowers with the stigmas and anthers removed before anthesis often set fruit. All of these phenomena suggest analogies to other rosaceous genera, such as *Rubus* and *Potentilla*, in which apomixis and hybridization are well documented. However, since irrevocable proof that these last phenomena occur in *Crataegus* has not yet been presented, the generalization given above is only a plausible hypothesis based on largely circumstantial evidence.

With the widespread clearing of the great forest that once extended from the Atlantic Coastal Plain to the prairies of midwestern North America, the habitats favorable for hawthorns were greatly expanded. It can be postulated that as the land was cleared, many discrete populations were able to expand their ranges (the nutlets are transported in the digestive tracts of birds and other animals) until their distributions were contiguous or overlapping. In such areas hybrids could have arisen, and if the hybrids were sexually sterile but able to set seed apogamously, local clones that superficially appear to be species (since they breed true from seed) could become established. Although the destruction of the eastern forests was largely by European settlers, Rousseau suggested that the *Crataegus* problem was created by the agricultural practices of the Iroquois Indians.

Probably no one has been more familiar with the myriad forms of *Crataegus* than was E. J. Palmer, whose knowledge was based on extensive field work, the examination of thousands of herbarium specimens, and the long-term observation of the more than 1400 plants (largely removed in the 1940's) representing nearly 700 forms of *Crataegus* that covered the Peters' Hill tract of the Arnold Arboretum. After his initial publication on *Crataegus* (in 1925, before the death of Sargent), Palmer adopted a more conservative approach, and his later papers and treatments reflect this philosophy. Palmer (1932) thought that ". . . a revision is urgently needed and that enough progress has now been made in understanding the genus to carry it out along conservative lines, that will neither seek to reduce arbitrarily species by throwing together as synonyms forms that are clearly recognizable, nor to maintain as species such as have been proven to have been based on inconstant distinctions or morphological characters too slight or obscure to be worthy of specific rank." Although Palmer never finished the revision, he did solve many nomenclatural and taxonomic problems. E. P. Kruschke, who has studied extensively the morphology of the *Crataegus* species found in the northern United States (especially Wisconsin), has made further contributions toward clarifying the complexities of the genus.

It seems likely that the genus will never be understood taxonomically until detailed studies that include cytology, genetics, and observations on reproductive biology, as well as morphology, have been made on a broad geographical basis. The situation was well summarized by Palmer (1943): "Much more experimental work is needed in many groups of plants before species problems can be resolved, and *Crataegus* offers one of the promising fields. It is also one of the most difficult. Some bright young man should start in it early in life, and it is hoped that he will have the background of a large endowment. In the meantime some adequate but conservative treatment of the genus is urgently needed, even though it may not be possible to dispose of all questions."

Because of the difficulty of identifying specimens of *Crataegus*, collectors should take special care to include both flowering or fruiting and vegetative shoots (making certain that both come from the same rootstock, since the branches of different species may intermingle) and to note the number of stamens and the color of the anthers, or the color of the fruit and the number of nutlets and the ease with which they may be separated from one another. If at all possible, flowering and fruiting collections should be made from the same plant.

The known intergeneric hybrids involving *Crataegus* and *Mespilus* bear the name × *Crataemespilus* Camus, with × *C. grandiflora* (Smith) Camus (*Crataegus monogyna* or *C. Oxyacantha* × *M. germanica*) and × *C. Gillotii* Beck (*Crataegus monogyna* × *M. germanica*). Graft-chimaeras between *Crataegus* and *Mespilus* are known as + *Crataegomespilus* Simon-Louis ex Bellair. A presumed graft-chimaera is also known between *Crataegus* and *Pyrus* (+ *Pyrocrataegus* Daniel; Weber was evidently referring to this chimaera when she mentioned an intergeneric hybrid between *Crataegus* and *Pyrus*).

Several species of *Crataegus* are commonly grown as ornamentals in the North Temperate Zone and are particularly attractive in spring, when in full bloom, and in autumn, when the leaves and plentiful fruits often take on brilliant colors. Although the fruits of a few species are eaten fresh or used in preserves and jellies, most are unpalatable and commonly are infested with weevils. However, few genera of plants are more important in the eastern United States than *Crataegus* in providing food during autumn and winter for birds and game animals.

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20. **Amelanchier** Medicus, Philosophische Botanik 1: 135, 155. 1789.

Deciduous, unarmed shrubs (sometimes stoloniferous or surculose) or trees with slender, terete branches; bark smooth, pale, on old trunks with shallow, scaly, longitudinal fissures; buds solitary, the lateral ones adpressed, fairly large, acute, sometimes with brightly colored and twisted scales; leaf scars elevated, narrowly crescent shaped or U-shaped with 3 bundle scars. Leaves alternate, petiolate; blades conduplicate [or imbricate] in bud, simple with serrate or rarely entire margins; stipules reddish, linear, caducous, leaving no scar. Inflorescences erect or drooping racemes [the flowers rarely solitary or paired] terminating growth of the season (the infructescences sometimes appearing axillary due to sympodial branching of the shoots), the flowers appearing shortly before or with the foliage; bracts pinkish, linear, deciduous. Flowers perfect, 5-merous. Calyx lobes erect, reflexed, or spreading at anthesis, persistent, imbricate in aestivation; floral tube campanulate to urceolate at anthesis, adnate to at least the bases of the carpels. Petals white [to pinkish], flaccidly spreading or narrowly ascending, obovate to lanceolate, tapering toward the base but usually not clawed, the margins entire or slightly erose at the apices, undulating, imbricate, inserted at the apex of the floral tube. Androecium usually of 20 stamens in 3 whorls; filaments free, persistent, unequal in length, shorter than the petals, inserted at the apex of the floral tube between the petals and a large, fleshy, 5-lobed nectar ring (the lobes opposite the petals); anthers dorsifixed. Gynoecium of 5 [or 2–4] carpels, abaxially partly to nearly completely adnate to the floral tube (the ovaries partly to completely inferior) and adaxially free with the margins unsealed but laterally connate; styles as many as the carpels, connate below to form a hollow column [or distinct], the lower part persistent; stigmas terminal, discoid; each carpel with 2 erect, hemianatropous ovules on an adaxial and basal or lateral placenta, the micropyle inferior, the 2 ovules soon ± separated by a partition that grows inward from the outer carpel wall. Fruit a dark blue to purple or nearly black (sometimes reddish when immature), globose or pyriform berry-like pome, often covered with a bloom, open at the apex, in section appearing 10 [or 4–8] locular due to the incomplete false septa; carpels ± adhering together, the locules with cartilaginous or membranaceous walls and surrounded by the enlarged, mealy to fleshy floral tubes. Seeds 2 per carpel and 1 per locule, or sometimes not all ovules maturing; seed coat membranaceous, smooth, dark brown; endosperm mostly absent; embryo erect, the cotyledons plano-convex, the radicle short, bent, inferior. TYPE SPECIES: *Mespilus Amelanchier* L. = *A. ovalis* Medicus. (Name perhaps derived from *amelanche*, the Provençal name of the European serviceberry, *A. ovalis*, evidently in reference to the honey-like taste of the fruit.) — SHADBUSH, SERVICEBERRY, SARVIS, JUNEBERRY.

About 20 to 30 species of the North Temperate region, with three species in Europe, northern Africa, and southwestern Asia; *Amelanchier asiatica* (Sieb. & Zucc.) Endl. (closely related to *A. arborea* of eastern North America) in Japan, southern Korea, and central China; no more than eight closely related species in western North America; perhaps nine species largely confined to the triangular area between Labrador, the western shores of Lake Superior, and New England; and seven species rather widely distributed in eastern North America and occurring in our area. *Amelanchier denticulata* (HBK.) K. Koch (western Texas to Guatemala) and *A. nervosa* (Decaisne) Standley (Mexico and Guatemala) have been placed in *Amelanchier* sect. MALACOMELES (Decaisne) Rehder or the genus *Malacomeles* (Decaisne) G. N. Jones. *Peraphyllum ramosissimum* Nutt., of the western United States, is closely allied to *Amelanchier*.

The taxonomic and nomenclatural complexities of *Amelanchier* perhaps are exceeded in the Rosaceae only by *Crataegus* and *Rubus*, and treatments of the genus differ greatly in the number of taxa recognized and the names applied to them. The bases for modern treatments of the American species are the extensive studies of Wiegand, Nielsen, Fernald, and Jones (whose revision has been critized for recognizing too few Eastern and too many Western species). Through their collective works, the entities occurring in our area can be ascertained fairly well, but their taxonomic status and names are still subject to debate. Wiegand (1912) summarized the problems in the genus: "*Amelanchier*, like *Rubus*, is a group in which it will never be possible to have the clearly cut condition found in so many genera where specimens will fall easily into one or another specific category. . . . It is no less difficult to determine what names should be applied to the species recognized. Synonymy here is very extensive and very much involved. It is complicated by the fact that many of the species of the earlier authors were undoubtedly aggregates, and also by the fact that several specific names were based upon material

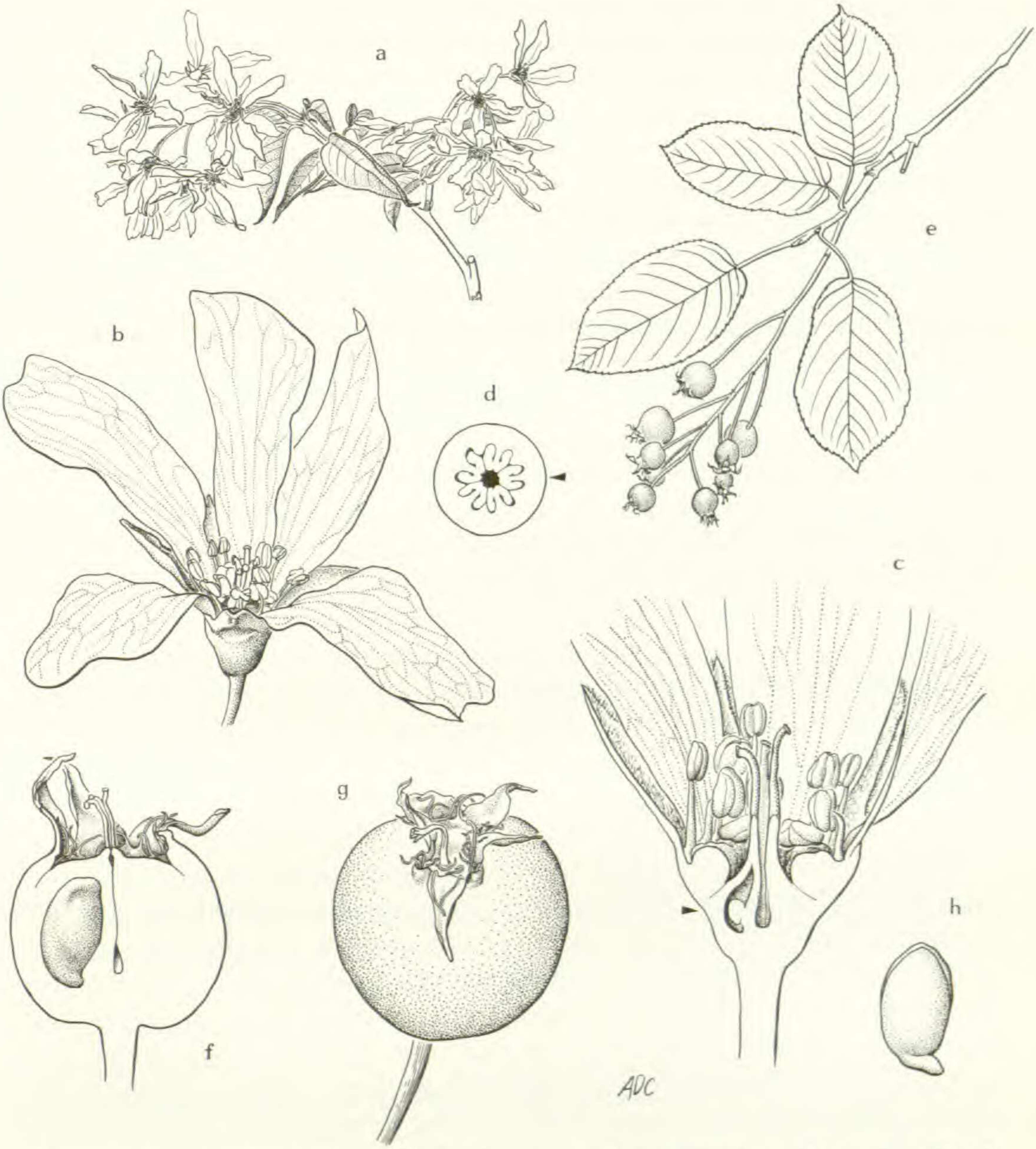

FIGURE 9. **Amelanchier.** a–h, *A. laevis*: a, flowering branchlet, × 1/2; b, flower, × 3; c, flower in vertical section to show placentation, carpels adaxially free, abaxially partly adnate to floral cup, note annular disc above carpels, cut at level of arrow in "d," × 6; d, cross section of ovary at level of arrow in "c," × 6; e, fruiting branchlet, × 1/2; f, nearly mature fruit in vertical section to show orientation of seed, calyx lobes, filaments, and persistent styles, × 3; g, mature fruit, × 3; h, embryo, oriented as in seed in "f," × 6.

from European gardens unlike any species now known to grow in the wild state. There is also some reason to believe that a few names were based on hybrid specimens."

All species in our area have leaves that are conduplicate in bud, racemose inflorescences, and five carpels with the styles at least basally connate. They can be divided into two broad groups (of no assigned taxonomic rank), the first of which is composed of species with the summits of the ovaries glabrous (or rarely slightly pubescent) and includes our two arborescent or fastigiately shrubby species that also have finely toothed, acuminate leaves and large flowers in nodding inflorescences. *Amelanchier arborea* (Michx. f.) Fernald, $2n = 68$,[14] with ascending branches, the leaves small and folded at anthesis and densely tomentose beneath when expanding, compact racemes, and maroon-purple, dry, insipid fruits, is represented in our area by three varieties. The typical variety (*A. canadensis* of Wiegand and others) has a wide habitat tolerance, occurring in rich to dry or rocky woods, thickets, or on slopes and bluffs from southwestern New Brunswick to southern Ontario, northern Michigan, and Minnesota south to northern Florida, Louisiana, and eastern Oklahoma and adjacent Kansas. Varietas *austromontana* (Ashe) Ahles, a short tree or tall shrub with smaller leaves, is evidently confined to southeastern Virginia and the mountains of western North Carolina, and Georgia. The identity and validity of this taxon need review. Jones clearly misinterpreted *A. austromontana* Ashe by selecting an "isotype" that does not match Ashe's description and locality and then considering that species a taxonomic synonym of *A. spicata* (Lam.) K. Koch. Also in need of further study is *A. arborea* var. *alabamensis* G. N. Jones, which differs from var. *arborea* by the somewhat pubescent apices of the ovaries. This character is usually associated with the "*sanguinea*" group of species and its occurrence in an obvious relative of *A. arborea* is unexplained; perhaps it is the result of hybridization. This peculiar variation occurs sporadically in southeastern Virginia, the Carolinas, Alabama, and Arkansas.

Amelanchier laevis Wiegand (*A. canadensis* of some authors, *A. arborea* var. *laevis* (Wiegand) Ahles), $2n = 68$, is characterized by spreading branches; leaves half-grown, reddish, and mostly glabrous at anthesis; rather loose inflorescences; and purple or nearly black, juicy, sweet pomes. Perhaps the most handsome of our eastern shadbushes, *A. laevis* is found in or at the borders of dry to moist woods or thickets, balds, rocky openings, and swamps from Newfoundland to southern Quebec, northern Wisconsin, Minnesota, and Iowa south to Ohio, Pennsylvania, and Maryland, extending in the Appalachians to Georgia and Alabama. The wood of this species is heavy and extremely hard, but the trees are too small for commercial lumbering.

The remaining species in our area with the ovary summit glabrous are shrubs with finely toothed and rounded or slightly mucronate mature leaves, erect inflorescences, and smaller flowers. *Amelanchier canadensis* (L.) Medicus (*A. oblongifolia* (Torrey & Gray) Roemer, see footnote 14; *A. Botryapium* (L. f.) Borkh.), $2n = 68$, tall, erect, clump-forming shrubs with the leaves heavily tomentose and only slightly developed at anthesis

[14] *Amelanchier canadensis* (L.) Medicus was applied by many early botanists to the species now called *A. arborea* and *A. laevis*; Wiegand (1912) restricted the name *A. canadensis* to the first of these two species, and this usage is still found in some manuals (such as Rehder). However, Fernald (1941) pointed out that *A. canadensis* (L.) Medicus should be applied to a tall, shrubby species that had previously been called *A. oblongifolia* (Torrey & Gray) Roemer.

and the racemes compact, is largely restricted to noncalcareous habitats on the Atlantic Coastal Plain from Georgia and Alabama to New England and southern Quebec, occurring inland to western New York. Plants with nearly entire leaves from the low pine barrens of southeastern Virginia have been segregated as var. *subintegra* Fernald. In a study of *A. arborea* (the identity of the plant studied should be checked since it is listed as having pubescent ovary summits), *A. laevis*, and *A. canadensis* in the Delaware River valley of New Jersey and Pennsylvania, Cruise found intermediates between *A. laevis* and *A. arborea* and between *A. laevis* and *A. canadensis*, but not between *A. arborea* and *A. canadensis*; it was postulated that *A. laevis* might have evolved as a result of introgression between the other two species, and Cruise felt it appropriate to treat the entire complex as a single variable species (*A. canadensis*).

Very similar to *A. canadensis*, and differing from it by the lower growth habit, the often purplish coloring of the well developed and nearly glabrous leaves at flowering time, the shorter and broader mature leaves, and the more open inflorescences, *A. intermedia* Spach is a somewhat doubtful taxon of often moist, calcareous habitats from Newfoundland to Michigan and Minnesota south to New England, Virginia, and the uplands of North Carolina. *Amelanchier obovalis* (Michx.) Ashe is a low stoloniferous shrub with compact racemes of flowers that precede the initially densely tomentose leaves. This species occurs in acid soils in dry, open pinelands, pocosins, and low woods, chiefly on the Coastal Plain but also in the mountains from Georgia and Alabama to South Carolina, North Carolina, inland Virginia, and southern New Jersey and Pennsylvania.

Members of the second group of species in our area have the top of the ovaries densely pubescent at anthesis, with some of the indumentum persisting on the fruit. *Amelanchier sanguinea* (Pursh) DC., $2n = 34$, a moderately tall shrub (sometimes weakly surculose) with few stems, reddish branches, coarsely toothed leaves, and lax, nodding inflorescences, is found on various noncalcareous substrata along river banks or in rocky, open woods or on slopes from southern Quebec to Thunder Bay District, Ontario, south to New England, New York, northern Ohio, Michigan, Wisconsin, Minnesota, and Iowa and disjunctly in the mountains of Virginia and North Carolina. *Amelanchier stolonifera* Wiegand, $2n = 34, 68$, a low stoloniferous shrub, with finely toothed leaves and dense, erect racemes, occurs in dry, sterile, rocky or sandy, often acidic open areas from Newfoundland to Thunder Bay District, Ontario, south to Nova Scotia, New England, Long Island, Virginia, the Carolinas, Michigan, and Minnesota. This species is often included, along with *A. humilis* Wiegand, in *A. spicata* (Lam.) K. Koch, a name disallowed by Fernald (1946a) for any North American shadbush (but Fernald's conclusion often has been ignored or disputed). The name *A.* × *spicata* is now frequently used for a commonly cultivated form that is probably a hybrid between *A. canadensis* and *A. ovalis* Medicus.

Numerous interspecific hybrids have been reported in *Amelanchier*; of the species in our area only *A. alabamensis*, *A. intermedia*, and *A. obovalis* are not yet known to hybridize with others. Each of our five other species ostensibly crosses with at least three species. *Amelanchier* × *grandiflora* Rehder[15] (*A. arborea* × *A. laevis*), $2n = 68$, perhaps the most beautiful shadbush with the largest flowers, is commonly cultivated in Europe and North America; in forma *rubescens* Rehder the flowers are pale purplish-pink in bud and tinged with pink when fully open. *Amelanchier alnifolia* (Nutt.) Nutt. and *Pyrus scopulina* (Greene) Longyear (*Pyrus* subg. *Sorbus*), both of the Pacific Northwest, have hybridized to produce × *Amelasorbus Jackii* Rehder, which has predominantly the floral characteristics of *Amelanchier.*

In 1931, Sax wrote that all the species that had been studied up to that time were diploids, while two hybrids were tetraploids. This generalization is occasionally quoted even today, but it is now quite incorrect, since the majority of species are tetraploids. Higher levels of polyploidy and aneuploidy are thus far unknown in *Amelanchier.*

Some of the variability in *Amelanchier* may be due partly to the same phenomena that occur in *Crataegus.* As the land in eastern North America was cleared, formerly isolated species expanded their ranges and were able to interbreed, with the hybrid progeny competing more successfully than the species in disturbed habitats. Certainly shadbushes found today in recently cleared or burned areas often have perplexing combinations of characters. However, unlike *Crataegus*, apomictic clones are not known in *Amelanchier.* Jones vehemently dismisses the commonly accepted hypothesis that hybridization regularly occurs between *Amelanchier* species and has been a major force in the evolution of infrageneric taxa. Instead, he speculates that "polyploidy may have played a more important part in the differentiation of genera and species in this subfamily . . . ."

Amelanchier species and hybrids are frequently cultivated in temperate regions for their graceful habit, the magnificent display of pure white flowers in early spring, the often abundant and colorful fruits that mature in mid-summer, and the fine shades of red or yellow the leaves assume in autumn. One common name of the eastern North American species, shadbush, comes from the fact that the plants are often in full bloom as the shad (*Alosa spidissima*) begin to ascend the streams to spawn. The fruits of all species, except *A. arborea*, are edible, but, because of their small size, are used mostly as fresh supplements on hiking and camping trips and in making jellies; many species of birds relish the mature fruits. Pemmican, the preserved, pressed-cake food of American Indians, contained dried buffalo or deer meat, fat, and saskatoon berries (the fruits of *A. alnifolia*). It has been suggested that serviceberries could become a major fruit crop in the basic soils of the Great Plains if a breeding program similar to Coville's work with blueberries (*Vaccinium* spp.) were undertaken.

[15] Schroeder (1968) considers *A.* × *grandiflora* to be a nomen ambiguum and places this under *A. Lamarckii* Schroeder.

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21. **Pyrus** Linnaeus, Sp. Pl. 1: 479. 1753; Gen. Pl. ed. 5. 214. 1754.

Deciduous or rarely semi-evergreen shrubs (sometimes rhizomatous) or small to medium-sized trees with slender to stout terete twigs; lateral spurs sometimes produced; unarmed or with axillary spines; bark smooth, longitudinally fissured, scaly, or forming plates; buds solitary, sessile, ovoid, oblong, or subconical, acute or obtuse, terminal buds often much larger than lateral ones; bud scales leaving prominent, narrow, semicircular scars; leaf scars low, elevated, or the nodes swollen below them, and linear, crescent shaped, or U-shaped with 3 or 5 (rarely 7) bundle scars. Leaves alternate, petiolate; blades conduplicate, convolute, or involute in bud, simple, with serrate to dentate [or rarely entire] margins, often lobed (the leaves of vegetative shoots more deeply lobed than those of flowering branches), or imparipinnate with serrate-margined leaflets; stipules small, deciduous, leaving no discernible scar. Inflorescences umbel-like racemes terminating lateral spurs or few to many-flowered corymbs terminating elongated shoots (the fruit seemingly axillary in subg. ARONIA), the flowers opening as the leaves expand or afterward; bracts linear, caducous. Flowers small to large, perfect, 5-merous. Calyx without an epicalyx, the lobes triangular, recurved or erect at anthesis, persistent [or deciduous], imbricate in aestivation; floral tube funnelform, campanulate, cup shaped, or urceolate at anthesis, adnate to the carpels. Petals white to pink [reddish or yellowish], spreading [or erect], ± equal, subcircular, broadly elliptic, or obovate with entire to crenate or erose margins, slightly to distinctly clawed at the base, sometimes pubescent on the adaxial surface, inserted at the edge of the floral tube, imbricate. Androecium of 15 to many stamens in one or several whorls; filaments free, persistent, unequal or equal in length, inserted at the apex of the floral tube, a nectar ring either not obvious or prominent and surrounding or covering the mouth of the floral tube; anthers red, purple, or yellow, dehiscing centrifugally or centripetally. Gynoecium of 2–5 carpels, abaxially half to completely adnate to the floral tube (the ovaries half to completely inferior) and adaxially and laterally half to completely connate; styles as many as the carpels, distinct to connate for more than half their length, often pubescent below, terminal on the adaxial margins of the carpels, persistent; stigmas discoid or in bands on the styles; each carpel with 2 (rarely more) erect, anatropous ovules on an adaxial and basal or lateral, sometimes elevated, placenta, the micropyle inferior. Fruit a red, yellow, green, purple, black, brown [or white] small to large, subglobose, ovoid, obovoid, or pyriform pome, the bases and apices sometimes depressed; carpels ± adhering together, the loculi with cartilaginous, membranaceous, or leathery [rarely almost stony] walls and surrounded by the enlarged, fleshy or mealy floral tubes, grit cells absent or abundant. Seeds one or two per carpel; testa membranaceous, smooth or with fine, longitudnal striations; endosperm essentially absent; embryo erect, the cotyledons plano-convex, the radicle short, straight, inferior. (Including *Malus* Miller, *Sorbus* L., and *Aronia* Medicus.) LECTOTYPE SPECIES: *P. communis* L.; see N. L. Britton, N. Am. Trees, 429. 1908. (Classical name of the pear tree; the spelling is often altered to *Pirus*, which is linguistically preferable but nomenclaturally unacceptable.)

A complex genus of perhaps 125 species in four subgenera of the North Temperate Zone. Although often treated as four distinct genera, it becomes exceedingly difficult to draw mutually exclusive generic limits when the group is examined on a world-wide basis. Additionally, all the subgenera, except subg. MALUS, freely hybridize. About sixteen species are indigenous and six exotic species are adventive or naturalized in North America; ten (including three introduced) occur in our area.

Subgenus PYRUS (*Pyrus* L. of many authors; sect. *Pyrophorum* DC.), pears, is composed of species with simple leaves involute in bud; large whitish flowers in few-flowered cymes that terminate short, lateral spurs; free styles; reddish anthers; and (in ours) pyriform fruits containing numerous grit cells. *Pyrus communis* L.,[16] the only representative of this subgenus in our area, has occasionally escaped from cultivation and become naturalized in thickets, fence rows, and clearings and along roadsides and the edges of woods in many regions of the United States. This "species" is now thought to be of hybrid origin with numerous European species in its genealogy, and it is known only in or as an escape from cultivation. According to Fernald, *P. pyrifolia* (Burm. f.) Nakai has spread from cultivation in southeastern Virginia; thus far this native of eastern Asia is not known to be adventive in our area.

[16] Several Europeans (see references in Staritsky) have recently applied the name *P. communis* L. to a wild Central European species and have used *P. domestica* Medicus for the cultivated pear.

The subgenus, often divided into four sections, contains more than thirty species distributed throughout most of temperate Eurasia. There are two morphologically, geographically, and perhaps ecologically distinct groups. The occidental pears (calyx persistent, pedicels fleshy, fruits pyriform) occur in western Eurasia from Turkestan to northern Africa and southern and western Europe, with the greatest diversity in Caucasia and the lands adjoining the western Mediterranean. The oriental pears (calyx deciduous, pedicels not fleshy, fruits subglobose) are plants of eastern Asia, from the Tien Shan and Hindu Kush to China, Korea, Japan, and Taiwan. They are particularly diverse in Yunnan and Hupeh provinces, China. *Pyrus Pashia* D. Don, of the Himalayas, is intermediate in morphology between the eastern and western groups. No species of this subgenus is native to the New World or to the Southern Hemisphere.

Pyrus communis hybridizes with *P. Aria* (L.) Ehrh. of subgenus SORBUS to produce what has been called × *Sorbopyrus auricularis* (Knoop) Schneider. The intergeneric hybrid between *P. communis* and *Cydonia oblonga* Miller is known as × *Pyronia Veitchii* (Trabut) Guillaumin. Graft-chimaeras between these two species are given the "generic" name + *Pirocydonia* H. Winkler ex Daniel. A presumed graft-chimaera between *Crataegus* and *Pyrus* is + *Pyrocrataegus* Daniel (*C. Oxyacantha* + *P. communis*).

All species of subgenus PYRUS that have been examined cytologically are diploid with $2n = 34$; polyploidy and aneuploidy are known only in cultivars. The study of Zielinski & Thompson (1967) supports Sax's theory on the allopolyploidy origin of the base number of $x = 17$ in the Maloideae (see subfamily account).

Several studies have shown that species of this subgenus are largely self-incompatible. Zielinski (1965) found that *Pyrus Fauriei* Schneider (a native of Korea) is quite self-compatible, but two clones of this species were reported by Westwood & Bjornstad to be self-incompatible but cross-compatible. According to Griggs & Iwakiri, the commonly cultivated 'Bartlett' pear (called 'Bon Chrétien William' in other countries) is largely sterile and does not set seed unless pollinated by pollen from other varieties, although seedless, parthenocarpic fruit are produced in the absence of cross-varietal pollination. Again, Westwood & Bjornstad were in contradiction, saying that the tetraploid 'Bartlett' was highly self-fertile. Interspecific sterility barriers are seemingly poorly developed in subg. PYRUS, since numerous hybrids are reported in the literature. Most of fifty-five interspecific crosses made by Westwood & Bjornstad were fertile. Apomixis is thus far unknown in this subgenus.

Subgenus MALUS (Miller) Pers. (*Malus* Miller; lectotype species: *Malus Malus* (L.) Britton = *P. Malus* L., see N. L. Britton, N. Am. Trees, 430. 1908), apples, with the leaves simple and involute, conduplicate, or convolute in bud, the flowers large, pink or reddish (at least in bud) and in few-flowered cymes that terminate short lateral spurs, the styles connate, the anthers yellow or red, and the fruits subglobose and usually lacking grit cells, includes perhaps thirty species in five sections in temperate Eurasia and eastern and western North America. Two sections are represented in the southeastern United States; the other three, which are largely Asiatic, present taxonomic problems critical in generic delimitation (cf. Browicz, Huckins).

Section MALUS S. F. Gray (*Malus* sect. *Calycomeles* Koehne; *Malus* sect. *Eumalus* Zabel) is composed of about ten species of Eurasia (Japan to the British Isles), with the greatest diversity in the region from Caucasia to the Hindu Kush and Tien Shan. The leaves are unlobed and involute in bud, the anthers are yellow, and the ovary is completely inferior and fused throughout its length to the fleshy floral tube. *Pyrus Malus* (*Malus pumila* Miller), the cultivated apple, probably of hybrid origin, persists after cultivation and evidently is reproducing from seed in many areas of the United States. Two Asiatic members of this section, *P. prunifolia* Willd. and *P. baccata* L., have spread from cultivation in eastern North America, but are not yet known to occur in our area.

Section CHLOROMELES (Decaisne) Robertson [17] (leaves conduplicate in bud, those of at least the vigorous shoots lobed; anthers reddish; apex of ovary in fruit pointed and free from the floral cup) is restricted to the eastern United States and adjacent Canada and includes our native crab apples. Although quite distinct from other sections of subg. MALUS, this section is very plastic, its members being particularly variable in leaf shape and degree of lobing, indumentum density, and fruit size. Yet, it is on the basis of these characters that nine species and numerous varieties have been recognized. The situation evidently has also been complicated by hybridization and perhaps introgression among the native crabs and between them and the cultivated apple. Until the taxonomy of the group has been more thoroughly studied, it seems best to recognize only three variable species and two named hybrids.

Pyrus angustifolia Aiton (*Malus angustifolia* (Aiton) Michaux; *M. bracteata* Rehder), the southern or narrow-leaved crab, is a spinescent shrub or small tree with abaxially glabrous or glabrescent calyx lobes and lanceolate to narrowly elliptic leaves with obtuse or short-mucronate apices. In the southern part of its range, it may be evergreen or semi-evergreen. The leaves of the flowering spurs are entire to serrate while those of rapidly growing vegetative branches are broader, much larger, and coarsely toothed or lobulate. Most abundant on the Coastal Plain from New Jersey to Florida, Louisiana, and southeastern Texas, *P. angustifolia* also occurs inland to Tennessee, Kentucky, and southeastern Missouri. *Pyrus coronaria* L. (*Malus coronaria* (L.) Miller, *M. fragrans* Rehder, *M. glabrata* Rehder,

[17] The proper combination under *Pyrus* does not appear to have been made previously for this section. *Pyrus* L. sect. **Chloromeles** (Decaisne) Robertson, comb. nov. *Malus* Miller subg. *Chloromeles* Decaisne, Nouv. Arch. Mus. Hist. Nat. Paris **10**: 155. 1874; *Chloromeles* (Decaisne) Decaisne, Fl. des Serres **23**: 156. 1881; *Malus* subsect. *Coronariae* Rehder in Sargent, Trees Shrubs **2**: 142. 1911; *Malus* sect. *Chloromeles* (Decaisne) Rehder, Jour. Arnold Arb. **2**: 48. 1920. TYPE SPECIES: *P. angustifolia* Aiton.

M. glaucescens Rehder, *M. lancifolia* Rehder), wild or sweet crab, distinguished by abaxially glabrous calyx lobes and broadly lanceolate to broadly ovate leaves with acute to acuminate apices, has a more northerly distribution, occurring from central New York to Wisconsin and southern Ontario, south to upland North Carolina, Tennessee, and Missouri. The leaves of the vegetative branches of this and the following species are usually distinctly lobed. In *Pyrus ioënsis* (Wood) Bailey (*Malus ioënsis* (Wood) Britton), Iowa or Bechtel crab, the calyx lobes and floral tubes are densely tomentose and the leaves are persistently pubescent below. This species enters our area only on the west, ranging from Indiana to Minnesota south to Kentucky, Louisiana, and the Edwards Plateau of Texas. The sweetly fragrant flowers of the eastern crab apples are pink in bud, becoming nearly pure white at anthesis, and finally turning dark pink or rose with age. At maturity the fruits are two to three centimeters in diameter, greenish yellow, with a fragrant, waxy coat and a tart, acidic taste.

Hybrids between the cultivated apple and the native eastern crabs have generally unlobed or weakly lobed leaves and fruits suffused to varying degrees with red and larger than 5 cm. in diameter. *Pyrus Malus* crosses with *P. angustifolia* and *P. coronaria* to produce *P.* × *platycarpa* (Rehder) Bailey, pro. sp., while hybrids of *P. Malus* and *P. ioënsis* are called *P.* × *Soulardii* Bailey, pro. sp.

Subgenus MALUS does not have the uniformity of chromosome number found in subgenus PYRUS. Diploid, triploid, and tetraploid species occur in the subgenus; pentaploidy, hexaploidy, and aneuploidy apparently exist only in cultivars and interspecific hybrids. Many of the reports are from cultivated material of doubtful identity, and possible correlations between chromosome number and the classification of the subgenus are uncertain. A thorough cytological study of our native crab apples seems in order, since their reported sporophytic chromosome numbers are: *P. angustifolia*, 34, 51, 68; *P. coronaria*, 51, 68; *P. ioënsis*, 34; *P.* × *platycarpa*, 51, 68; and *P.* × *Soulardii*, 34.

There are numerous reports in the literature on reproductive abnormalities of apples. Unreduced gametes evidently are produced rather frequently, and, although the role of such gametes in nature is a matter of conjecture, they have been of considerable importance in the production of new polyploid cultivars. Apomixis occurs in several species of sects. MALUS and SORBOMALUS. In most cases the plants are ostensibly facultative apomicts, with the embryo sacs developing from unreduced megaspores. The triploid *P. hupehensis* Pamp. is almost an obligate apomictic with the embryo sacs produced aposporously; the aposporous egg cells are occasionally fertilized by pollen from other species, giving rise to hybrids of a higher polyploid level. Pseudogamy also occurs in this subgenus.

Interspecific hybridization is common within subgenus MALUS. Species of sect. CHLOROMELES cross with members of sect. MALUS but not with those of sect. SORBOMALUS; hybrids between sects. MALUS and SORBOMALUS occur.

The cedar-apple rust-fungus (*Gymnosporangium juniperi-virginianae*) is endemic to eastern North America and is remarkable for the correlation between its hosts and their taxonomic relationships. All species of *Pyrus* sect. CHLOROMELES harbor the spermogonial and aecial stages of the fungus (only *P. Malus*, *P. fusca*, and possibly *P. communis* and *P. glauca* are other such hosts), and all hosts of the telial stage belong to *Juniperus* sect. SABINA (with the exception of the doubtful host *J. communis*).

Subgenus SORBUS (L.) Reichenb. (*Sorbus* L.; lectotype species: *Sorbus Aucuparia* L. = *Pyrus Aucuparia* (L.) Gaertner; see A. Rehder, Bibliogr. Cult. Trees Shrubs, 252. 1949, and G. K. Brizicky, Jour. Arnold Arb. **49**: 502–508. 1968 [18]), mountain ashes, encompasses more than eighty species (in five sections) of the temperate regions of the Northern Hemisphere. The species that approach members of the other subgenera of *Pyrus* morphologically make it difficult to define this variable group concisely. In subg. SORBUS the leaves are simple or odd-pinnate and conduplicate, convolute, or involute in bud; the flowers are smallish and in many-flowered compound corymbs terminating short or long shoots (inflorescences rarely on short, woody spurs); the anthers are yellow or red; and the fruits are small to large, globose, ovoid, or pyriform pomes with grit cells either absent or abundant.

Perhaps eight species occur in North America: *Pyrus americana* (Marshall) DC. is restricted to the eastern part of the continent; two species occur in Greenland, as well as on the American mainland; three species and five varieties are native to western North America; *P. sambucifolia* Cham. & Schlecht., an Asiatic species, extends to the westernmost Aleutian Islands; and *P. Aucuparia* is introduced from Europe. All these species belong to sect. SORBUS (L.) S. F. Gray (*Aucuparia Medicus*, nom. illegit.; *Sorbus* sect. *Aucuparia* K. Koch; *Sorbus* subg. *Aucuparia* Kovanda; *Sorbus* sect. *Eusorbus* Boiss.) (leaves imparipinnate, ovary of 2 to 4 or rarely 5 carpels that are only basally connate), a holarctic group with a particularly large number of species in western Asia.

Pyrus americana (*Sorbus americana* Marshall; *P. microcarpa* (Pursh) DC.), $2n = 34$, American mountain ash, rowan-tree, or missey-moosey, occurs primarily in moist woods from Newfoundland and Côte Nord, Quebec, to northeastern Minnesota, southward to northern Illinois, Pennsylvania, and New Jersey, and extending in the mountains to Virginia, Tennessee, the Carolinas, and Georgia. A related species, *P. decora* (Sargent) Hyland, $2n = 34$, with villous, rather than glabrescent, inner bud scales and broader, less acute, firm leaflets, has a more northern distribution ranging from southern Greenland and Labrador to northern Ontario and southeastern Manitoba, south to Nova Scotia, northern New England, New York, Ohio, Indiana, Iowa, Wisconsin, and Minnesota. Restricted to alpine or subalpine regions in southern Greenland, coastal Labrador, Newfoundland, the Gaspé Peninsula, and the mountains of northern New

[18] Brizicky's argument that, since *Sorbus domestica* L. does not agree with the essential features of the generic protologue, *S. Aucuparia* L. must be taken as the type species of *Sorbus* L. seems to be correct.

England, *P. groenlandica* (Schneider) Robertson,[19] $2n = 68$, is distinguished from *P. decora* by the membranaceous leaflets that taper from near the middle to a prolonged acumination. Löve & Löve hypothesized that this species is an allopolyploid between *P. americana* and *P. decora*. *Pyrus Aucuparia*, $2n = 34$, a small tree with permanently pubescent branchlets, leaflets, and peduncles, and with bright orange fruit, has spread from cultivation and become naturalized in many parts of Canada and the northern United States (see Hultén, 1971, under family references). Thus far this species, the widespread European parallel of *P. americana*, is not known to be adventive in our area.

The other sections of subgenus SORBUS are sect. CORMUS (Spach) Robertson,[20] with *Pyrus Sorbus* Gaertner (*Sorbus domestica* L.; *Pyrus domestica* (L.) Smith, non Medicus), of southern Europe and northern Africa; sect. ARIA (Pers.) DC. (*Sorbus* subg. *Aria* Pers.; *S.* sect. *Aria* (Pers.) Dumort.; *Hahnia* Medicus), a taxonomically difficult group of about 35 species that is particularly diverse in Caucasia; sect. TORMINARIA DC. (*Sorbus* sect. *Torminaria* (DC.) Dumort.; *Sorbus* subg. *Torminaria* (DC.) K. Koch), with *P. torminalis* (L.) Ehrh., of southern, western, and central Europe, and northern Africa; and sect. CHAMAEMESPILUS (Medicus) Lindley (*Chamaemespilus* Medicus; *Sorbus* subg. *Chamaemespilus* (Medicus) Koch; *Sorbus* sect. *Chamaemespilus* (Medicus) Schauer), with *P. Chamaemespilus* (L.) Ehrh. in the mountains of central and southern Europe.

Interspecific barriers to hybridization are weakly developed in some species of subg. SORBUS. *Pyrus americana* crosses with *P. Aucuparia* and *P. Aria* (L.) Ehrh., of this subgenus, and with *P. floribunda* and *P. melanocarpa*, of subg. ARONIA (see discussion under subg. ARONIA for other hybrids between these two subgenera). *Pyrus Aria* also hybridizes with *P. communis* of subg. PYRUS. Hybrids occur between members of sect. ARIA and sects. SORBUS, TORMINARIA, and CHAMAEMESPILUS, but members of the last three sections do not interbreed. *Pyrus Sorbus* (sect. CORMUS) rarely crosses with other species. An intergeneric hybrid is × *Amelasorbus Jackii* Rehder (*Amelanchier florida* Lindley × *Pyrus scopulina* (Greene) Longyear). Kovanda (1961) mentions hybrids between members of subg. SORBUS and *Crataegus, Cotoneaster*, and *Mespilus*. It is interesting that most of the known intergeneric and intersubgeneric hybrids have arisen spontaneously in nature, botanical gardens, or nurseries; attempts to make such hybrids artificially often fail.

Subgenus SORBUS is taxonomically difficult in Europe and has been studied in some detail in Scandinavia and the British Isles. There are four

[19] **Pyrus groenlandica** (Schneider) Robertson, comb. nov. *Sorbus americana* Marshall var. *groenlandica* Schneider, Bull. Herb. Boiss. II. **6**: 314. 1906. *Sorbus decora* var. *groenlandica* (Schneider) Jones; *Pyrus decora* var. *groenlandica* (Schneider) Fernald; *Sorbus groenlandica* (Schneider) Löve & Löve.

[20] *Pyrus* L. sect. **Cormus** (Spach) Robertson, comb. nov. *Cormus* Spach, Hist. Nat. Vég. **2**: 96. 1834. *Sorbus* sect. *Cormus* (Spach) Boiss.; *S.* subg. *Cormus* (Spach) Ducharte; *S.* subg. *Sorbus* Kovanda; *Pyrus* b. *Cormus* Ascherson & Graebner.

wide-ranging, diploid, sexually reproducing primary species: *Pyrus Aria, P. Aucuparia, P. torminalis,* and *P. Chamaemespilus* (*P. Sorbus* is also diploid but is evidently not involved in the evolution of the numerous biotypes). It has been hypothesized that diploid and partly sterile hybrids were produced between *P. Aria* and the other three species, and allotetraploids were formed from these F_1 hybrids. In some instances, autotetraploids were derived from the diploid species, and triploid plants resulted from crosses between diploids and tetraploids. Individual polyploid plants can be apomictic, and, since some are only facultatively so, backcrossing with either parental species (or with another species not in the hybrid's genealogy) is possible. This evolutionary pattern is remarkably similar to that postulated by Babcock & Stebbins for the western North American species of *Crepis* (see discussion in Liljefors, 1955, p. 105).

Subgenus ARONIA Reichenb. (*Aronia* Medicus, nom. cons. prop., non Mitchell; type species: *Mespilus arbutifolia* L. = *Pyrus arbutifolia* (L.) L. f.; *Pyrus* sect. *Adenorachis* DC.; *Adenorachis* (DC.) Nieuwland), chokeberries, comprises three closely related species of eastern North America that are shrubs with finely serrate leaves with numerous glands along the upper midrib, smallish flowers in simple to more or less compound inflorescences that generally terminate long shoots (these shoots may branch sympodially and the inflorescences then appear to be axillary), and small, berrylike fruits. The three taxa of subg. ARONIA have been treated variously as three species, one species with three varieties, or two species with one of them having two varieties. The group is often considered a distinct genus or placed under *Sorbus* L.

Pyrus arbutifolia (*Aronia arbutifolia* (L.) Ell.; *Sorbus arbutifolia* (L.) Heynhold), $2n = 34, 68$, a shrub with reddish, long-persistent fruits, glandular calyx lobes, dull green leaves that turn red in autumn, and tomentose branchlets, pedicels, and lower leaf surfaces, ranges from Florida, Georgia, Alabama, Mississippi, Louisiana, and eastern Texas northward to New York, New England, and Newfoundland. In our area this species is most frequently encountered on the Coastal Plain in low woods, swamps, bogs, thickets, savannahs and damp pine barrens. Usually a rhizomatous shrub one to three meters high, some individuals may be small trees to six meters in height, and dwarf forms of bogs, pine barrens and subalpine regions are few stemmed and less than a half meter tall. Several varieties and forms based on habit, leaf size, and indumentum density have been described; these need to be studied.

Pyrus melanocarpa (Michaux) Willd. (*Aronia melanocarpa* (Michaux) Ell.; *A. nigra* Koehne; *Sorbus melanocarpa* (Michaux) Heynhold), $2n = 34$, is usually shorter than the above species and can be recognized by the black, short-persistent fruits, somewhat glandular calyx lobes, lustrous leaves that mostly turn brown in autumn, and mostly glabrous branches and leaves. This species occurs in similar or drier habitats from Newfoundland to northwestern Ontario and Minnesota southward to New England, Virginia, the Carolinas, Georgia, Tennessee, northwestern Alabama and Kentucky; in our area it is most common in the Piedmont.

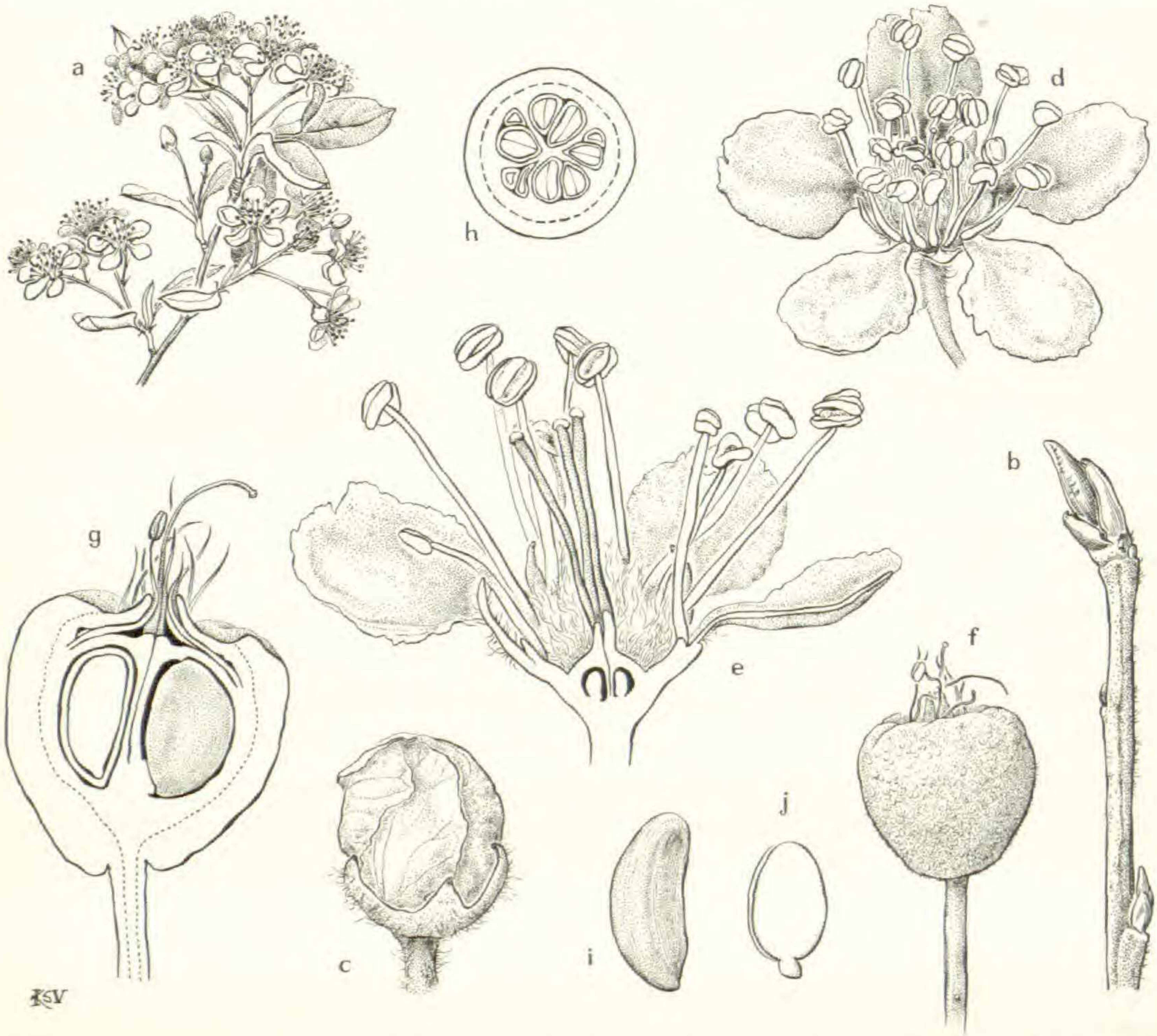

FIGURE 10. **Pyrus** subg. **Aronia.** a–j, *P. arbutifolia*: a, tip of branchlet with inflorescences, × 1/2; b, twig with terminal and lateral winter buds, × 2; c, flower bud, petals imbricate, × 5; d, flower, × 3; e, flower in vertical section to show placentation and insertion of petals and stamens, × 5; f, fruit, note persistent calyx lobes, filaments, and styles, × 3; g, fruit in vertical section, seed on left in section, dotted line shows division between tissues of floral cup and carpels, × 5; h, cross section of fruit, some seeds aborted, × 3; i, seed, oriented as in fruit, × 6; j, embryo, oriented as in seed, × 6.

Pyrus floribunda Lindley (*Aronia prunifolia* (Marshall) Rehder; *A. atropurpurea* Britton; the proper combination under *Sorbus* does not appear to have been made) is similar to *P. arbutifolia*, differing by its purple, long-persistent fruits, mostly eglandular calyx lobes, and moderately pubescent vegetative parts. It is found in similar habitats from Newfoundland, southward to New England, Virginia, North Carolina, Georgia, and Florida, west to Ontario (Algome District), Michigan, Indiana, Kentucky, Tennessee, Alabama, and Missouri. This plant, clearly intermediate between *P. arbutifolia* and *P. floribunda*, has been considered to be either a distinct species or a variety of each of the others. Hardin, in an excellent review of the chokeberries (which he recognized as the genus *Aronia*), concluded that *A. prunifolia* is of hybrid origin "by means of ancient as well as current hybridization and introgression . . ." Evidence was presented by Hardin that agamospermy probably occurs in *P. floribunda*, and this "could effectively stabilize the hybrid forms, and aid the distribution beyond the zone of sympatry of the parental species." Hardin preferred to recognize only *A. arbutifolia* and *A. melanocarpa* including *A. prunifolia* (*P. floribunda*) in the latter species.

Because the species of this subgenus are so variable and closely related, interspecific hybrids are difficult to detect; Fernald lists a hybrid between *Pyrus floribunda* and *P. melanocarpa*. There are numerous intersubgeneric hybrids between subgenera ARONIA and SORBUS (when these are maintained as genera, such hybrids have the name × *Sorbaronia* Schneider); *Pyrus arbutifolia* crosses with *P. Aucuparia* and with *P. Aria*; *P. floribunda* with *P. americana*, *P. Aucuparia*, and *P. decora*; and *P. melanocarpa* with *P. americana*, *P. Aucuparia*, and *P. Aria*. In these hybrids, the stamens are pinkish, the leaves have glands on the upper midrib, and, if either *P. americana*, *P. Aucuparia*, or *P. decora* is one of the parents, the leaves are partly pinnate; in addition, the plants are somewhat sterile and meiosis is irregular.

Pyrus is of considerable economic importance. Pears and apples are major fruit crops in temperate regions and are consumed fresh, dried, or canned or converted into juice (unfermented or fermented), jelly, or purée. Numerous species of pears, apples, mountain ashes, and chokeberries are widely grown as ornamentals for both their abundant flowers and colorful fruits. Although not a major timber crop, the wood of the arborescent species is used in musical instruments and tool handles. Apple wood is prized for golf-club heads. A homeopathic treatment has been made from the astringent inner bark of *P. Aucuparia*. During the winter months, the fruit of the native and introduced species is a primary food for many kinds of animals, especially birds.

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Subfam. AMYGDALOIDEAE Torrey & Gray, "Subordo" (Subfam. Prunoideae Focke)

Four genera, *Prunus* L., sensu lato, *Maddenia* Hooker f. & Thomson (five spp. in China and the Himalaya), *Osmaronia* Greene (*O. cerasiformis* (Torrey & Gray) Greene, western North America), and *Prinsepia* Royle (four spp., eastern Asia). Members of this subfamily are trees or shrubs with simple leaves, carpels inserted at the base of, but free from the floral cup, drupaceous, 1-seeded fruits, and a base chromosome number of eight. *Osmaronia*, because of its flowers with usually five carpels and seeds with folded cotyledons, is sometimes separated as tribe Osmaronieae Rydb. The taxonomic position of *Prinsepia* (style lateral or subbasal; ovules erect, the micropyle inferior) is debatable; Sterling proposed tribe Prinsepieae ("Prinsepioideae") to include it.

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22. **Prunus** Linnaeus, Sp. Pl. 1: 473. 1753; Gen. Pl. ed. 5. 213. 1754.

Deciduous or evergreen trees or shrubs, sometimes producing root sprouts; bark, twigs, and leaves with smell and taste of bitter almond due to presence of cyanogenic glycosides; bark initially reddish-brown, thin, smooth, easily peeled off in layers, remaining that way or breaking into scaly plates, the lenticels pale, usually elongating transversely; branches sometimes spinescent; buds solitary or 3, terminal one present or absent, the bud scales several, imbricate, the inner ones colored, accrescent. Leaves simple, often glossy above, convolute or conduplicate in bud, petiolate, the margins usually serrate, sometimes entire or spine-toothed; prominent, variously sized and shaped glands usually occurring on petioles or at base of leaf blades; stipules paired, free from the petiole, small, early deciduous; leaf scars elevated, with 3 vascular traces. Flowers 5-merous, mostly perfect, in racemes terminating shoots of the season, in racemes from axils of leaves of the previous season, in corymbs or umbels from branchlets of the previous season (appearing before or with the leaves), or solitary and sessile or stalked. Calyx ebracteolate, the lobes triangular, imbricate in bud; floral tube campanulate, tubular, urceolate, or cup shaped, usually circumscissile deciduous; disc lining the floral tube, thin, often colored. Petals white to pink, spreading, quickly falling, orbicular to elliptic, the margins entire or erose, the bases short clawed, inserted at the outer edge of the floral tube [petals indistinguishable from calyx lobes in some species of subg. LAUROCERASUS]. Stamens usually 15–20 (10–80) in two or more whorls and in multiples of 5, perigynous at the outer edge of the floral tube; filaments filiform, exserted, the inner shorter than the outer; anthers small, dorsifixed. Gynoecium of one carpel inserted at the base of, but free from, the floral tube; ovary glabrous to densely pubescent; style terminal, elongated; stigma capitate, discoid, or emarginate; ovules 2, pendulous, the micropyle superior. Fruit a 1-seeded drupe, sometimes sulcate and/or glaucous, the mesocarp fleshy and indehiscent to dryish and dehiscent, usually edible, the endocarp hard, indehiscent, nearly globose or compressed, smooth or textured; seed filling stone, the coat membranaceous, the radicle superior. Base chromosome number 8. (Including *Amygdalus* L., *Armeniaca* Duh., *Cerasus* Mill., *Laurocerasus* Duh., *Padus* Mill., *Persica* Duh., and *Pygeum* Gaertn.) LECTOTYPE SPECIES: *P. domestica* L., see Britton, N. Am. Trees, 480. 1908. (The ancient Latin name of the Plum.) — PLUM, CHERRY, PEACH.

Maybe 200 species mostly of the North Temperate region, particularly abundant in North America, eastern Asia, western Asia, and southern Europe. Unlike most Rosaceae, *Prunus* is well represented in the subtropics and tropics, and the distribution of the genus extends southward in the Old World through Malesia to northern Queensland and in the New World through Central America to Chile and Brazil. The species fall into several reasonably distinct groups that are often treated as genera. However, when studied on a world-wide basis, the morphological discontinuities between the groups decrease, and it becomes more logical to recognize only one inclusive genus with several subgenera (see discussions in McVaugh and Kalkman).

Several systems of subgeneric classifications have been proposed (see enumeration in McVaugh), and there is no general agreement as to how many subgenera or sections should be recognized, how these should be delimited, or what species to include in each. The genus was studied extensively by Koehne, but his classification schemes do not seem to reflect natural relationships well. The basic system proposed by Rehder, in which five subgenera and twelve sections are recognized, is perhaps the one most widely used today. About thirteen species representing four subgenera are indigenous to the southeastern United States; a number of exotic species are cultivated, and some of these persist or escape.

Subgenus PADUS (Miller) Focke (leaves deciduous, conduplicate in bud; inflorescences many-flowered racemes terminating leafy shoots of the current year) includes about 20 species mostly of Eurasia, especially China and Japan, with two species in the Americas. *Prunus serotina* Ehrh., $2n = 32$, black cherry, is a variable species that occurs from Florida to Arizona, Mexico, and Guatemala northward to Nova Scotia, New Brunswick, southern Quebec, southern Ontario, Minnesota, and North Dakota; it has escaped from cultivation in Central and South America and in Europe. This species has been reviewed by McVaugh, who recognizes five subspecies, two of which occur in our area: subsp. *serotina* (eastern North America west to Lake Superior, the Dakotas, and eastern Texas; disjunct in Mexico and Guatemala) and subsp. *hirsuta* (Ell.) McVaugh (Alabama and Georgia; including *P. alabamensis* Mohr, *P. Cuthbertii* Small, and perhaps *P. australis* Beadle). Subspecies *eximia* (Small) McVaugh occurs on the Edwards Plateau and the Belcones Escarpment of Texas; subsp. *virens* (Wooton & Standley) McVaugh ranges from Trans-Pecos Texas to Arizona, south to Baja California and Mexico; and subsp. *Capuli* (Cav.) McVaugh, capulín, is from the highlands of southern Mexico and Guatemala (introduced farther south). The wood of *Prunus serotina* is pale reddish-brown (sapwood yellow), close-grained, light, fairly hard and strong, and has working qualities that make it one of the finest cabinet woods of temperate North America, second only to black walnut (*Juglans nigra*).

Prunus virginiana L., $2n = 32$, choke cherry, occurs from Newfoundland to Saskatchewan south to North Carolina, Tennessee, Missouri, Kansas, Oklahoma, and Texas; also in the West from the Dakotas to New Mexico and west to California and British Columbia. Three varieties can be recognized (see Hitchcock *et al.*, family references); plants in eastern North America belong to var. *virginiana*. *Prunus serotina* and *P. virginiana* are quite similar in many ways; closer examination shows numerous differences, and they have been placed in different sections. Plants of *P. serotina* can be large trees 30 m. tall with trunks 2 m. in diameter (most large ones now logged), the bark is aromatic, the leaves are narrow, tapering ovate, shiny above, and crenate-serrate with callous teeth, the calyx lobes are acute, and the floral cups persist below the nearly black drupes. *Prunus virginiana* is a shrub or small tree with nonaromatic bark, leaves that are obovate or broadly elliptic, dull above, and sharply serrate, obtuse calyx lobes, circumscissile dehiscent floral cups, and deep red or purple fruits. *Prunus Padus* L., European bird cherry, with larger flowers, adaxially pubescent floral cups, and strongly sculptured stones, is cultivated in our area, but it is not known to be naturalized.

Subgenus LAUROCERASUS (Duhamel) Rehder (plant evergreen, leaves often entire; racemes usually solitary in axils of leaves of the previous year, the peduncles leafless) is composed of about 75 species mostly of tropical Asia and tropical America with a few species in southern Europe and southern North America; two species occur in our area. Kalkman recently reviewed the Asiatic members, noting that all American species could be placed in one distinct, unnamed section. *Prunus caroliniana* (Miller) Aiton, $2n = 32$, Carolina cherry laurel, is found on the outer Coastal Plain from southern North Carolina to midpeninsular Florida westward to eastern Texas (reported from Bermuda by Sargent). Plants are evidently rare in nature, but the species is commonly cultivated in the southern United States as a specimen tree or trimmed to a hedge. *Prunus myrtifolia* (L.) Urban (*P. sphaerocarpa* Sw.), West Indian cherry, is found in pinelands and hammocks in southern Florida; it is widely distributed in tropical America, ranging from Florida and the Bahama Islands to the Greater Antilles, Montserrat, Trinidad and Tobago, and Mexico to Brazil. Both *P. caroliniana* and *P. myrtifolia* can have functionally staminate flowers at the base of the racemes. Two species of this subgenus are cultivated in our area, *P. Laurocerasus* L., $2n = 144$, 170–180, cherry laurel, and *P. lusitanica* L., $2n = 64$, Portugal laurel. Native to California and Baja California are *P. ilicifolia* (Nutt. ex Hooker & Arn.) Walp. and *P. Lyonii* (Eastw.) Sargent.

Subgenus CERASUS (Miller) Focke (flowers solitary or in few-flowered corymbs often on short, lateral shoots; fruits not sulcate, glaucous, or pubescent, the stone globose or ovoid, mostly smoothish), cherries, includes numerous species of temperate Eurasia and North America; Rehder recognized seven sections. Two species occur indigenously in the southeastern United States, and several others are cultivated, sometimes becoming naturalized. *Prunus pumila* L., (including *P. cuneata* Raf., *P. susquehanae* Willd., and *P. Besseyi* Bailey) $2n = 16$, sand cherry, is a variable species that occurs mostly in sandy or rocky situations from New Brunswick to Manitoba and North Dakota southward to Delaware, North Carolina, Indiana, Wisconsin, Kansas, Colorado, and Wyoming; it has recently been reported from Arkansas (Gary Tucker, Arkansas Polytechnic College, personal communication). *Prunus pensylvanica* L. f., $2n = 16$, bird-, pin-, or fire-cherry, occurs from Labrador to British Columbia south to Virginia, the mountains of North Carolina and Tennessee, Illinois, Iowa, South Dakota, Colorado, and Montana; this is a pioneer species in recently burned or cleared areas. Reportedly escaped from cultivation in our area are *P. Avium* L., $2n = 16$, sweet cherry (the commonly sold 'Bing' cherry is a cultivar of this species), *P. Cerasus* L., $2n = 32$, sour cherry, and *P. Mahaleb* L., $2n = 16$, Mahaleb or perfumed cherry, all of southern Europe and western Asia.

Subgenus PRUNUS [*Prunophora* Focke] (flowers solitary or in few-

FIGURE 11. **Prunus** subg. **Padus** (a–i), subg. **Cerasus** (j–l), and subg. **Laurocerasus** (m). a, *P. virginiana*: flowering branch with racemes terminating leafy branchlets of current year, × 1/4. b–i, *P. serotina*: b, fruiting branch, × 1/2; c, tip of raceme, × 3; d, vertical section of flower (petals removed) to show perigynous insertion of calyx lobes and stamens, carpel solitary, 2-ovulate, × 10; e, vertical section of ovary at right angles to that in "d" to show pendulous ovule, micropyle superior, × 20; f, stone from drupe, × 3; g, cross section of stone, wall hatched, cotyledons unshaded (seed coat too thin to show), × 3; h, seed removed from stone, × 3; i, embryo, oriented as in seed in "h," × 3. j–l, *P. pensylvanica*: j, tip of branch with corymbose inflorescences, × 1/2; k, tip of short shoot showing leaf bases with glands and stipules, × 3; l, flower, × 3. m, *P. caroliniana*: spinulose-serrate leaf form, × 1/2.

flowered umbels from axillary buds on growth of previous years; fruit sulcate, glaucous or pubescent, the stone compressed) includes about 30 species of Eurasia and North America. The wild plums of North America constitute a distinct section, sect. PRUNOCERASUS Koehne (flowers usually three or more, fruit not pubescent, stones smoothish); seven of the fourteen species occur in the southeastern United States. *Prunus americana* Marsh., $2n = 16$, wild plum, occurs from northern Florida west at least to Arkansas, northward to New England, southern Ontario, Wisconsin, and Manitoba. Plants from the southern part of the range westward to Texas and northern Mexico have the leaves pubescent below to varying degrees, the plants evidently do not often produce root suckers, and the fruit is bluish to purple-red; these plants perhaps are best placed in *P. mexicana* S. Watson (including *P. lanata* auct., not Sudw., *P. americana* var. *lanata* auct., *P. arkansana* Sarg., *P. Palmeri* Sarg., *P. reticulata* Sarg., and *P. tenuifolia* Sarg.), big-tree plum, Mexican plum. These two species need to be studied in detail to ascertain their distinctiveness and distribution (see Correll & Johnston, Man. Vasc. Pl. Texas; Steyermark, Fl. Missouri; Shinners). *Prunus angustifolia* Marsh., $2n = 16$, chickasaw plum, ranges from central Florida to Texas, northward to Maryland, Delaware, and Arkansas; *P. geniculata* Harper, from central Florida, is probably a depauperate form of this species.

The other species of sect. PRUNOCERASUS in our area are *Prunus gracilis* Engelm. & Gray, Oklahoma plum (Arkansas, Oklahoma, and Texas); *P. hortulana* Bailey, $2n = 16$, wild goose plum (southern Indiana to Iowa southward to western Tennessee, northern Alabama, Missouri, Arkansas, and Oklahoma); *P. Munsoniana* Wight & Hedrick, $2n = 16$, wild goose plum (Ohio, Kentucky, and Tennessee to Louisiana, Kansas, Oklahoma, and Texas); and *P. umbellata* Ell. (including *P. injuncta* Small, *P. mitis* Beadle, and *P. tarda* Sarg.), hog or flatwood plum, black sloe (southern North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, and southern Arkansas). Numerous varieties of plums have been derived in recent years from the native American species, although it is difficult to judge how important these are commercially.

Old World species cultivated in the southeastern United States include *Prunus domestica* L., $2n = 48$, plum, *P. insititia* L., $2n = 48$, bullace, damson plum, *P. cerasifera* Ehrh, $2n = 16$, cherry plum, *P. spinosa* L., $2n = 32$, sloe, all of subg. PRUNUS sect. PRUNUS; *P. Armeniaca* L., apricot, $2n = 16$, of subg. PRUNUS sect. ARMENIACA (Lam.) W. D. J. Koch; and *P. Amygdalus* Batsch, $2n = 16$, almond and *P. Persica* (L.) Batsch, $2n = 16$, peach, nectarine. Only the last species is known to be naturalized in our area.

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